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MYCOLOGIA

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VOL. L MARCH–APRIL, 1958 NO. 2

MARINE FUNGI. IV. LULWORTHIA AND CERIOSPOROPSIS

T. W. JOHNSON, JR.[1]

(WITH 43 FIGURES)

The two commonest marine ascomycetous genera in restricted localities and in world-wide distribution are *Lulworthia* Sutherland and *Ceriosporopsis* Linder. Wood panels submerged in sea water (2–8 weeks or more) usually become infested with a considerable population of these two genera. Driftwood, stems of tidewater or intertidal angiosperms, and untreated or partially decayed pilings also harbor abundant populations of these fungi. Members of *Lulworthia* and *Ceriosporopsis* often appear on wood even before the more rapidly developing of the Fungi Imperfecti.

Taxonomically significant variation is exhibited by these fungi. Coincident with increasing studies on marine fungi is an increase in the number of species described in the two genera. Although the genera are circumscribed by distinct features, species are often not easily delimited, or may be separated only by such inconspicuous characteristics as ascospore length and appendage length.

Two hundred and fifty-seven collections of *Lulworthia* and *Ceriosporopsis* were made in the past two years in the North Carolina coastal

[1] This study was made possible by a National Science Foundation Grant, G-2324, and supplemental funds from the Duke University Council on Research. The comments and reviews by Drs. L. S. Olive and S. P. Meyers are gratefully acknowledged. Special thanks are accorded Dr. F. A. Wolf for assistance in preparing the Latin diagnoses.

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region. This paper presents the results of a comparative study of these collections. Observations and measurements were made on ascocarps from the substratum (submerged in sea water) and, in part, on fructifications appearing in unifungal culture on sea water agar. The former are emphasized since I believe this represents the more natural expression of the fungi. Collections were made from driftwood, tidewater angiosperm culms, and various species of wood submerged as test panels (Johnson, **1956**). Variants of established species are noted.

LULWORTHIA

A brief historical résumé of the genus was presented by Miss Wilson (**1956**), Cribb and Cribb (**1955**), and Johnson (**1956**). The genus is best known under the name *Halophiobolus* Linder (Barghoorn and Linder, **1944**), a name antedated by *Lulworthia*. Two systems of species differentiation have been proposed. Linder divided the genus (*Halophiobolus*) into two groups on the basis of neck length; further species delimitation was based primarily on color and texture of the perithecial wall, or on ascospore length. Meyers (**1957**), on the other hand, segregated species of *Lulworthia* entirely on two characteristics: length of the ascospore, and length of the terminal spore appendages. Meyers concluded from field observations and culture studies that neck length was too variable to be a significant diagnostic characteristic. Similarly, he found perithecial color and shape, of lignicolous species, to be influenced by the wood texture and grain. The significance of the foregoing discussion will be apparent in the notations on species.

LULWORTHIA SALINA (Linder) Cribb and Cribb, Papers Univ. Queensland Dept. Bot. **3**(10): 80. 1955.

This species has been reported from the Beaufort region (Johnson, **1956**). A subsequent collection (from submerged yellow-poplar panels) is a variant with dark-brown, concolorous perithecia. Two collections of another variant (on basswood panels) are worthy of mention. The dark-brown, necked ascocarps are depressed-globose to broad-ellipsoid. Ascospore size is reasonably similar to that of *L. salina*, but appendage length is slightly smaller, 3.5–7.8 μ, with a median at 4.5 μ. In this respect the variant is necessarily nearer *L. medusa* (Johnson, **1956**).

Meyers (**1957**) considers *Lulworthia opaca* and *L. longirostris* synonymous with *L. salina*, basing the decision primarily on similarity of spore- and appendage-size. This disposition ignores neck length, which, if retained as a valid segregating characteristic, prevents such

synonymy, since *L. opaca* and *L. longirostris* have long-necked perithecia. The fungus on poplar panels has ascospore size well within the range of the aforementioned species, but the appendages are slightly longer: 7.5–11.2 μ, with the median at 8.7 μ. In appendage length the variant of *L. salina* agrees with *L. floridana* (Meyers, **1957**).

If Meyers's synonymy is accepted, *Lulworthia salina* is an extremely variable species. Neck length in the *salina-opaca-longirostris* complex cannot be entirely ignored. None of the ascocarps in the very large Beaufort collection have necks exceeding ¼ the height of the perithecial venter. Furthermore, the short-necked condition is not due to abrasion and decomposition of the ascocarp as the surrounding wood decays and sloughs away. A few perithecia of each variant of *L. salina* have developed in unifungal culture; these are without necks, or with short, broad-conic ones.

LULWORTHIA FLORIDANA Meyers, Mycologia **49**: 515. 1957.

This species was collected in abundance on submerged rootstocks of *Spartina alterniflora*. The necks are short and broad-conic, or lacking; perithecia are globose, innate, and black or dark-brown throughout. Meyers reports elongate or papillate necks for the species. The fungus on *Spartina* produces short or much reduced necks exclusively; this may well be due to the nature of the substratum. Superficially, *L. floridana* resembles *L. halima*, but ascospore-appendage length and the nature of the necks readily separate the two. Spore-appendage length in my material of *L. floridana* is more variable than reported by Meyers. Spores from the collection have an appendage-length range of 8–35 μ, with a predominant range of 8–11 μ. The median length is 9.4 μ, compared with 8.0 μ reported by Meyers. The difference is not significant, but is a basis for questioning species separation exclusively on appendage length. Spore-appendage length in the Beaufort material of *L. floridana* is nearly the same as that reported for *Halophiobolus* (i.e., *Lulworthia*) *rufus* (Wilson, **1956**). The perithecia are, however, very much different.

LULWORTHIA MEDUSA var. BISCAYNIA Meyers, Mycologia **49**: 516. 1957. (FIGS. 1–3).

Ascospore length in the fungus collected on submerged pine panels is slightly larger (299–394 μ) than that of either *L. medusa* var. *medusa* or var. *biscaynia*. The ascospore appendages are only slightly smaller.

The necks are very long, usually 2–3 times as long as the venter diameter. Perithecia are completely innate. Two to five necks may be produced by a single ascocarp; infrequently, one or more of the necks may branch.

Lulworthia purpurea (Wilson) comb. nov. (FIG. 20).

Halophiobolus purpureus Wilson, British Myc. Soc. Trans. **39**: 403. 1956.

This is a readily distinguishable species, particularly in spore-appendage length (10–18 μ). Allowing for variation in ascocarp shape, the only difference between the Beaufort collection and that described by Miss Wilson is that the appendages of the former are more sharply tapering. Very rarely, the spore appendages only attain a length of 6 μ.

Lulworthia rufa (Wilson) comb. nov. (FIGS. 21, 22).

Halophiobolus rufus Wilson, British Myc. Soc. Trans. **39**: 405. 1956.

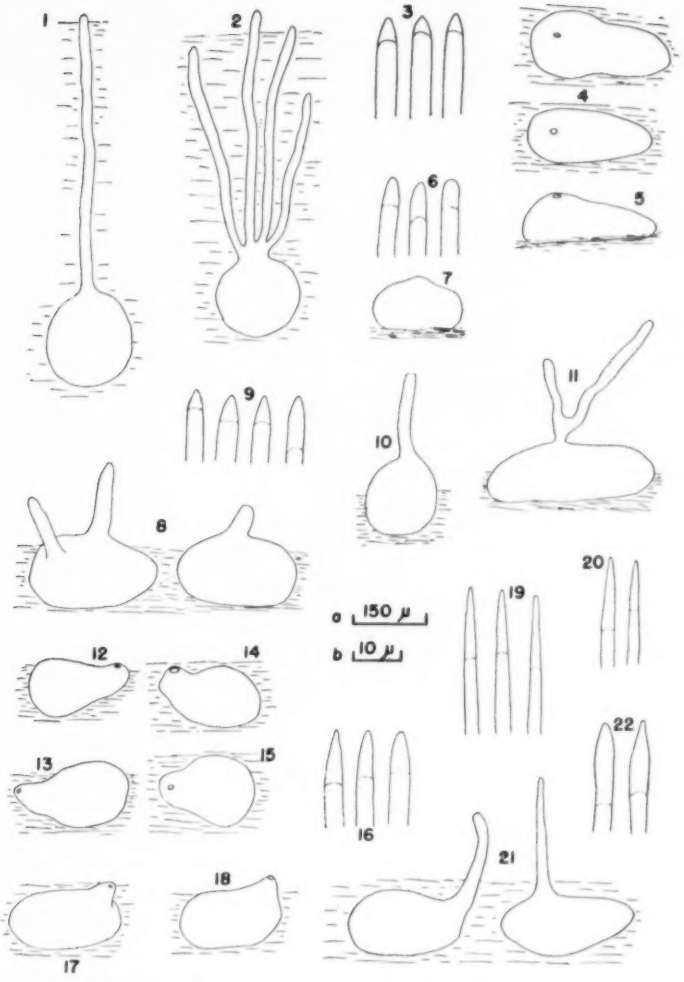
This fungus, on yellow-poplar panels, occasionally produces pyriform or globose, centric-necked ascocarps rather than "swan-shaped" fructifications (FIG. 21) as described by Miss Wilson. The ascospores are slightly shorter than indicated in the original description. In this species, at least, perithecial shape is apparently an insignificant diagnostic characteristic, whereas spore-appendage length and perithecial coloration are distinctive.

Lulworthia rotunda sp. nov. FIGS. 4–7.

Peritheciis superficialibus vel partim innatis, supra brunneis, infra flavo-brunneis, elongato-ovoideis, depressis, termino ostiolato longiore quam termino alterno, 245–288 μ longis, 100–148 μ diam. ab termino ostiolato; collis brevibus, lato-papilliformibus vel nullis; aparaphysatis. Ascis elongato-fusiformibus, irregularibus, deliquescentibus. Ascosporis filiformibus, hyalinis, aseptatis, 365–455 × 2.8–4.2 μ, appendiculis inclusis; appendiculis 4.2–(4.7–)8.4 μ longis, apice lato-rotundato vel aliquantulo pyramidato.

Hab. in ligno Tiliae, quod submersum erat per 51 dies, contra terminum orientale insulae "Carrot Island," Carolinae borealis, Julio 20, 1956 (TYPE).

Perithecial shape in *Lulworthia rotunda* is different from that of any other species. Viewed from above, the ascocarps are either obovate or pyriform (FIG. 4); from the side, they are nearly obovate with a flattened base. The fungus typically produces short necks or none (FIGS. 5, 7). There is no evidence that the perithecia are actually short-



Lulworthia. FIGS. 1–3. *L. medusa* var. *biscaynia*. Perithecia and spore appendages. FIGS. 4–7. *L. rotunda*. FIG. 4. Top view of perithecia. FIG. 5. Side view of perithecium. FIG. 6. Spore appendages. FIG. 7. End view of perithecium. FIGS. 8–11. *L. conica*. Perithecia and spore appendages. FIGS. 12–16. *L. submersa*. FIGS. 12–14. Side view of perithecia. FIG. 15. Top view of perithecium. FIG. 16. Spore appendages. FIGS. 17–19. *L. attenuata*. Perithecia and spore appendages. FIG. 20. *L. purpurea*. Spore appendages. FIGS. 21, 22. *L. rufa*. Perithecia and spore appendages. FIGS. 3, 6, 9, 16, 19, 20, 22, scale b; others, scale a.

necked through abrasion. The few ascocarps produced in culture are without necks.

Ascospore-tip length is nearly identical with that of *Lulworthia medusa* var. *biscaynia*, but the spores of *L. rotunda* are slightly longer. There is little similarity in perithecial shape among *L. rotunda*, *L. medusa* var. *medusa*, and var. *biscaynia*. Ascospore-appendage shape (FIG. 6) is unique among the species in the genus.

Lulworthia conica sp. nov. FIGS. 8–11.

Peritheciis partim innatis, supra atro-brunneis, in parte submersa hyalinis, subglobosis vel depresso-globosis, interdum sphericis, 210–250 μ longis, 152–210 μ diam.; collis brevibus vel longo-cylindraceis, centricis vel excentricis, aliquantulo-pyramidatis ad apicem flavum ac rotundatum, interdum bi-ostiolatis; aparaphysatis. Ascis non visis, deliquescentibus. Ascosporis filiformibus, hyalinis, aseptatis, 503–579 × 2.8–3.5 μ, appendiculis inclusis; appendiculis 4–(5.1–)10 μ, cuspidatis ad apicem rotundatum.

Hab. in ligno Piceae, quod submersum erat per 51 dies, contra terminum orientale insulae "Carrot Island," Carolinae borealis, Augusto 21, 1956 (TYPE).

Except for perithecial pigmentation, *Lulworthia conica* superficially resembles *L. grandispora*. Ascospores are slightly shorter, and the terminal appendages are longer in *L. conica* than in *L. grandispora*. Perithecial shape and coloration are similar to some forms of *L. salina*, but spore length is different. The spore appendages are characteristic for *L. conica*, in shape but not in length. Perithecial pigmentation is similar to that of *L. longirostris*, but in other features, *L. conica* is different.

Lulworthia submersa sp. nov. FIGS. 12–16.

Peritheciis innatis, pallido-brunneis ad ostiolum hyalinis, elongato-ovoideis, pyriformibus vel ovatis, 197–229 μ longis, 125–146 μ diam:; collis lato-conicis vel lato-cylindraceis, brevibus, lateralibus; aparaphysatis. Ascis elongato-clavatis vel fusiformibus, deliquescentibus. Ascosporis filiformibus, hyalinis, aseptatis, 208–229 × 3.5–5 μ, appendiculis inclusis; appendiculis 8.5–(9.3–)12.5 μ, conicis, pyramidatis, ad apicem rotundatis.

Hab. in ligno Aceris, quod submersum erat per 86 dies, apud signum alveum, Radio Island, prope Beaufort, Carolinae borealis, Julio 29, 1956 (TYPE).

The perithecia of this fungus are distinctive. In submerged panels of spruce and maple, the ascocarps are completely immersed; often even the ostiole is below the substrate surface. Pigmentation, similarly, is distinctive; the venter is light brown except for the few hyaline cells around the ostiole. The ostiolar end is always composed of simple,

large, pseudoparenchymatous cells. Usually, the ascocarps are ovoid or ovate, with the lateral "neck" merging gradually with the perithecial venter. The "neck" is slightly curved upward toward the substrate surface (FIGS. 12–14). The perithecia develop in a resupinate position with respect to the substratum, both in wood and in unifungal culture on seawater agar.

The perithecia of *Lulworthia submersa* bear a superficial resemblance to those of *L. rotunda;* in the latter, however, the ostiole is apical and the perithecia are not completely innate. None of the described species or reported variants have the perithecial type characteristic of *L. submersa.* Shape of the ascospore tips is similar to that of *L. cylindrica, L. salina, L. purpurea,* and *L. floridana.* The length of the spore appendages is very nearly the same as that of *L. floridana* and *L. rufa.* Spore length of *L. submersa* falls within the range described for *L. halima, L. floridana,* and *L. purpurea.* Considering only the ascospores, therefore, *L. submersa* is near *L. floridana;* in ascocarp characteristics the two species are unlike.

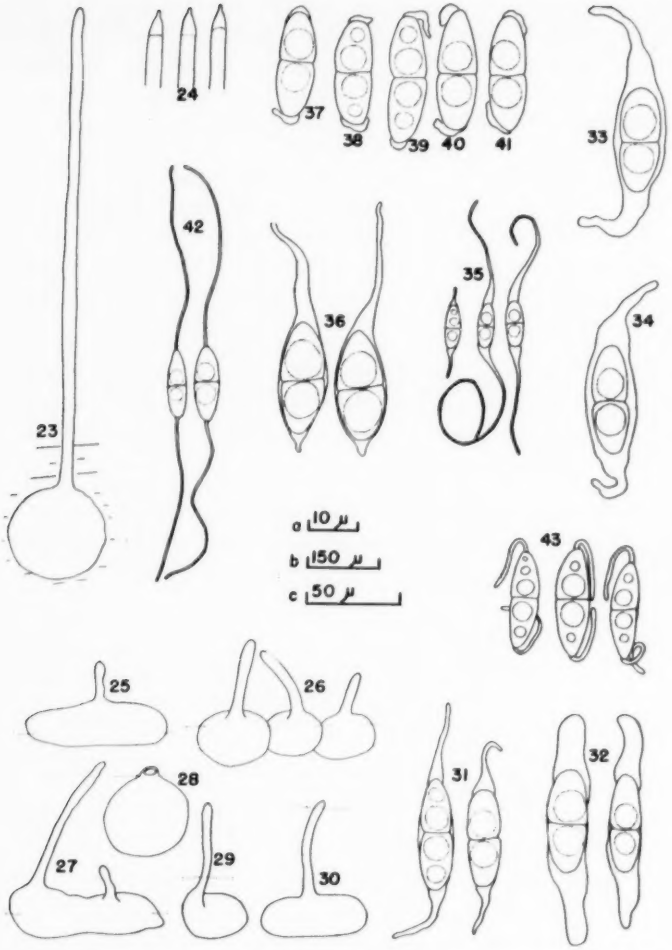
The sole use of spore and appendage length as discriminatory features for *Lulworthia submersa* is not admissible. Emphasis must be placed on the perithecial characteristics, which contrast readily with those of any other species in the genus.

Lulworthia attenuata sp. nov. FIGS. 17–19.

Peritheciis innatis, supra atro-brunneis, infra flavo-brunneis vel hyalinis, elongatis, ovoideis, depresso-globosis, 190–236 μ longis, 101–126 μ diam.; collis lato-conicis, nigris, excentricis vel lateralibus; aparaphysatis. Ascis fusiformibus, deliquescentibus. Ascosporis filiformibus, hyalinis, aseptatis, 132–168 × 3.5–4.9 μ, appendiculis inclusis, attenuatis, ad basem appendicularum 2.4 μ diam; appendiculis 13–(14.3–)17 μ, longo-conicis, ad apicem leviter rotundatis.

Hab. in ligno Liriodendri, quod submersum erat per 181 dies, prope insulam "Piver's Island," Carolinae borealis, Januario 19, 1957 (TYPE).

Ascospores tapering gradually from a broader middle toward narrower ends are characteristic of *Lulworthia salina* as well as *L. attenuata.* The spore-appendage length of the latter is twice that of the former, although total spore length is nearly the same. Furthermore, perithecial shape differentiates the two species. The short-neck condition (FIGS. 17, 18) of *L. attenuata* is not due to abrasion or decomposition. In culture, the fungus consistently produces perithecia with short, broad-conic necks. Typically, *L. salina* has long-necked ascocarps, even though the necks are often shortened by decomposition; in some forms,



Lulworthia and *Ceriosporopsis*. FIGS. 23, 24. *L. grandispora* var. *apiculata*. Perithecium and spore appendages. FIGS. 25–36. *C. halima*. FIGS. 25–30. Variations in position and shape of perithecia. FIG. 31. "Typical" ascospore. FIGS. 32–36. Variations in ascospore appendages. FIGS. 37–41. *Ceriosporopsis* sp. Ascospores. FIGS. 42, 43. *C. hamata*. Ascospores. FIGS. 23, 25–30, scale b; figs. 35, 42, scale c; others, scale a.

however, short-necked perithecia are produced exclusively. The lateral-necked perithecia of *L. submersa* differ from those of *L. attenuata* in shape and coloration. Spore-appendage length but not spore length of *L. attenuata* approximates that of *L. rufa*. Perithecial shape and neck length are much different. The same features distinguish *L. attenuata* from *L. purpurea*.

The new fungus is suggestive of *Lulworthia salina* in a restricted sense, but very closely allied to *L. salina* when variants of the latter are included. The only significant feature distinguishing the two is spore-appendage length; whether this characteristic will remain as a critical diagnostic one will depend on what future monographic studies reveal.

Lulworthia grandispora var. **apiculata** var. nov. FIGS. 23, 24.

Peritheciis innatis vel partim innatis, atro-brunneis vel brunneis, globosis vel raro subglobosis, 204–306 μ diam.; collis longis, cylindraceis interdum ramosis, concoloribus, centricis; aparaphysatis. Ascis fusiformibus, hyalinis, deliquescentibus. Ascosporis filiformibus, hyalinis, aseptatis, 510–650 × 3.5–4.8 μ, appendiculis inclusis, attenuatis, acutiusculis, ad basem appendicularum 2.4 μ diam.; appendiculis 4–(5.2–)7 μ longis, conicis, apiculatis.

Hab. in ligno Aceris, quod submersum erat per 53 dies, "Newport River," prope "Morehead City," Carolinae borealis, Julio 22, 1956 (TYPE).

Two characteristics distinguish this fungus from *Lulworthia grandispora* (Meyers, **1957**): tapering ascospores and apiculate spore appendages. Although spore length is comparable to that of *L. grandispora* var. *grandispora*, the spore shape is distinctive, and has not been reported for any species or variety in the genus. Approximately the middle one-half of the spore is of equal diameter throughout. The terminal quarters of the spore taper gradually to a very small diameter at the appendage juncture. This differs from the spores of *L. attenuata*, in which tapering begins at the midpoint. The terminal appendages of *L. grandispora* var. *apiculata* are always apiculate (FIG. 24).

Appendage length is comparable to that of *Lulworthia medusa* var. *biscaynia*. In common with *L. grandispora* var. *grandispora*, the necks of the variety *apiculata* are extremely long (but occasionally broken off, *in situ*) reaching a maximum length of 1216 μ.

The number of species now in *Lulworthia* dictates that a key to taxa be available as a convenience in identification. The following tentative key utilizes synonymy according to Meyers (**1957**). Spore length is inclusive of the terminal appendages; appendage measurements are of length.

KEY TO SPECIES OF LULWORTHIA

A. Perithecium without a neck or with a short, broad-conic or papilliform one; neck shorter than height of perithecial venter ..... B
A. Perithecium with a definite, well-developed, cylindrical neck; neck longer than height of perithecial venter I
B. Neck lateral; appendages 8.5–(9.3–)12.5 μ ..... *L. submersa*
B. Neck centric or eccentric C
C. Spores tapering toward ends; appendages 13–(14.3–)17 μ ..... *L. attenuata*
C. Spores not tapering ..... D
D. Perithecium depressed, ostiolar end of greater diameter than opposing end; appendages 4.2–(4.7–)8.4 μ ..... *L. rotunda*
D. Perithecium not depressed; ostiole centric ..... E
E. Ascospores less than 100 μ long ..... *L. fucicola*
E. Ascospores more than 100 μ long ..... F
F. Ascospores 150–500 μ long ..... G
F. Ascospores greater than 500 μ long; appendages 3.6–(3.7–)4.3 μ ..... *L. grandispora*
G. Ascospores 150–200 μ long, appendages 7.5–(8.7–)11.2 μ ..... *L. salina*
G. Ascospores 230–425 μ long ..... H
H. Ascospores 230–320 μ long, appendages 7–(8–)14 μ ..... *L. floridana*
H. Ascospores 320–425 μ long; appendages 7–8.4 μ ..... *L. medusa*
I. Ascospores tapering toward ends ..... J
I. Ascospores not tapering toward ends ..... K
J. Ascospore appendages apiculate; appendages 4–(5.2–)7 μ; ascospores 510–650 μ long ..... *L. grandispora* var. *apiculata*
J. Ascospore appendages not apiculate; appendages 3.5–(8.7–)11.2 μ; ascospores 150–200 μ long ..... *L. salina*
K. Perithecium purple-brown or orange-red, changing to dark brown in neck, pale fuscous in venter L
K. Perithecium not purple-brown or orange red; brown or yellow-brown throughout, or dark brown to pallid brown in neck, hyaline or pallid yellow in venter ..... M
L. Perithecium purple-brown; ascospores 190–292 μ long; appendages 10–(18–)26 μ ..... *L. purpurea*
L. Perithecium orange-red, changing to dark brown above, pale fuscous below; ascospores 216–284 μ long, appendages 10–12 μ ..... *L. rufa*
M. Ascospores less than 100 μ long ..... *L. fucicola*
M. Ascospores greater than 100 μ long ..... N
N. Perithecium brown, dark brown, or black above, hyaline below ..... O
N. Perithecium concolorous, or if not, dark above, yellowish below ..... P
O. Apex of neck yellow; ascospores 500–570 μ long; appendages 4–(5.1–)10 μ ..... *L. conica*
O. Apex of neck black or brown; ascospores 320–425 μ long; appendages 7–8.4 μ ..... *L. medusa*
P. Ascospores greater than 500 μ long ..... *L. grandispora*
P. Ascospores less than 500 μ long ..... Q
Q. Appendages 7–(9–)35 μ ..... *L. floridana*

Q. Appendages 3–7 μ ..... R
R. Ascospores more than 320 μ long; appendages 3.6–(4.4–)7 μ; perithecia innate ..... *L. medusa* var. *biscaynia*
R. Ascospores less than 320 μ long; appendages 3–4 μ; perithecia partially innate or superficial ..... *L. halima*

CERIOSPOROPSIS

Ceriosporopsis (Linder, in Barghoorn and Linder, **1944**) is contrasted with *Ceriospora* by perithecial characteristics, and by the deliquescent asci and ascospore appendages. Furthermore, the former is aparaphysate as opposed to *Ceriospora*. Meyers (**1956**) comments on the extreme variability of perithecial venter shape, and length and number of necks. Although he suggests that perithecial characteristics are not sufficiently fixed to be used in species separation, he observes that spore size and nature of the appendages also show intergradations among collections. Miss Wilson (**1954**), similarly, by a comparative study of *Ceriosporopsis halima* and *Ceriosporopsis cambrensis*, notes certain variable characteristics in the former not mentioned by Linder. Meyers justifiably questions the validity of establishing *Ceriosporopsis* species on the basis of spore size.

Four species are known: *Ceriosporopsis halima* Linder, *C. barbata* Höhnk and *C. hamata* Höhnk (**1955**), and *C. cambrensis* Wilson (**1954**). Admittedly, the differences among these species are negligible, with the exception of *C. halima* and *C. cambrensis*.

CERIOSPOROPSIS HALIMA Linder, *In* Barghoorn and Linder, Farlowia **1**: 409. 1944. (FIGS. 25–36).

My illustrations indicate, partially, the extent of spore variation in this ubiquitous species. Perithecial shape is extremely variable, showing innumerable gradations between globose and ellipsoid (FIGS. 25–30). Neck length of ascocarps referable to this species is not a significant diagnostic characteristic.

In what may tentatively be accepted as its "typical" expression, the ascospores of *Ceriosporopsis halima* are hyaline, one-septate, biguttulate, with a single, gelatinous, tapering appendage at each end (FIG. 31). The ascospore wall is characteristically constricted at the faint midseptum. In the majority of spores a thin gelatinous sheath covers the entire spore. The sheath may be lacking or very thick (FIGS. 33, 34). Spore size is variable, and in several large developments of *C. halima* the spores from a single perithecium exceeded in size range that of the other three described species. Spore-appendage length is likewise ex-

tremely variable (FIG. 35), and is possibly determined by the rate of deliquescence. Spores from one collection had opposing appendages consistently of unequal length (FIG. 36).

CERIOSPOROPSIS HAMATA Höhnk, Veröffent. Inst. Meeresfors. Bremerhaven **3**: 210. 1955. (FIGS. 42, 43).

Although ascospore and perithecial size and perithecial shape of this species are the same as in some variants of *C. halima*, the spore appendages are very much different. In *C. halima* the terminal processes taper gradually from a broad base to a rounded apex; in *C. hamata* the appendages are narrow and cylindrical throughout (FIG. 43). Appendge length, however, is not a decisive diagnostic characteristic for *C. hamata*, since extremely long appendages (FIG. 42) occur rather commonly in some ascocarps. Separation of *C. halima* and *C. hamata* turns completely on appendage shape. Such a distinction is questionably consequential, hence *C. hamata* is only tentatively accepted as a valid taxon.

CERIOSPOROPSIS AND LENTESCOSPORA

Two collections of fungi, tentatively placed in *Ceriosporopsis*, were made on decaying stems of *Spartina alterniflora* dredged from 8 meters, Intracoastal Waterway, Newport River (salinity 22.9‰), North Carolina, and on submerged maple panels. The ascocarps are innate, short-necked (or without necks) and ellipsoid to globose. Except for coloration (hyaline or yellow-brown), the ascocarps are equally referable to *Lentescospora* or *Ceriosporopsis*.

The two genera are essentially analogous in perithecial characteristics, and, to a lesser extent, in spore appendages. The spores of *Lentescospora* (Linder, in Barghoorn and Linder, **1944**) have hyaline, gelatinized, thick-walled end portions. Such processes appear as "caps" over the ends of the spores. Thus, the only difference (taking into account ascocarp variability) between *Lentescospora* and *Ceriosporopsis* is that of the spore appendages. The spores of the fungus on *Spartina* and maple are capped by a gelatinous substance, but frequently this material is free at one end from the spore wall (FIG. 40). Such spores suggest those of a *Ceriosporopsis* with vestiges of deliquescing appendages. Spores on which the gelatinous cap adheres by its entire length to the spore wall (FIGS. 38, 41) are, on the contrary, recognizable as those of *Lentescospora*. Some spores have one appendage suggestive of those of *Ceriosporopsis*, the other identical with those of *Lentescospora* (FIGS. 37, 39). Linder commented on the similarity of these genera; the

North Carolina material is indicative of an even closer similarity than Linder suspected.

SUMMARY

Eight species (four new) and two varieties (one new) of *Lulzworthia* are described. Two species and several variants of *Ceriosporopsis* are reported. The similarity of spore appendages in *Ceriosporopsis* and *Lentescospora* is discussed.

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ACCIDENTAL ISOLATION OF TRICHOPHYTON MENTAGROPHYTES FROM THE FLOOR OF A SCHOOLHOUSE

FLORANTE C. BOCOBO AND ARTHUR C. CURTIS

(WITH 2 FIGURES)

A proven case of cryptococcosis was seen in the Department of Dermatology, University of Michigan Hospital, and attempts were made to trace the possible source of infection. At the onset of his illness, the patient was working as a janitor in the Foster School of Ypsilanti, Michigan. This is a rambling, one-story schoolhouse built during the Second World War. In view of the recent reports of the isolation of *Cryptococcus neoformans* in nature (**1**, **4**, **5**), samples of soil and floor dust from the schoolhouse were obtained: Sample 1 and Sample 2 were soils from under drains, Sample 3 was from the sweepings gathered in the bag of a vacuum cleaner used to clean the floors, and Sample 4 was from dirt accumulated on a motor-driven rotary floor brush.

Each sample was suspended in physiological saline solution in a 100 ml graduate with vigorous agitation and left to settle at room temperature. After 3 hours, portions of the top layers of the suspensions were inoculated on duplicate Sabouraud's-dextrose-agar slants, both with and without penicillin and streptomycin. One set of the cultures was left at room temperature and the duplicate set, at incubator temperature. These were examined periodically for growth and discarded after six weeks. For animal inoculation, one ml of the supernatant layer of each suspension was injected intraperitoneally into mice. Each suspension was used to inoculate five mice. Pieces of the livers, spleens and lungs of animals that died were planted on Sabouraud's dextrose agar slants. The remaining animals were sacrified after three weeks and the organs similarly planted.

The cultures directly planted with the samples did not show any growth of pathogenic fungi, and most eventually became overgrown with contaminants. However, *Trichophyton mentagrophytes* was isolated from the livers or spleens of two animals inoculated with portions of Sample 3, composed of vacuum cleaner sweepings. The macroscopic and microscopic features of these isolates were characteristic (FIGS. 1,

2). Their pathogenicity was proven by positive takes on five guinea pigs, a week after suspensions of the cultures were rubbed on the skin abraded with sterile sand paper. KOH examinations of the scales from these lesions were positive for hyphae and the organism was recovered on cultures.

In order to test the viability of *Trichophyton mentagrophytes* when introduced into the peritoneal cavity of the mouse, the following experiments were performed. A moderately thick suspension of spores in physiological saline solution was made from a vigorously growing colony of the original isolate and 0.25 ml injected intraperitoneally into 25 mice. The animals were divided into groups of five. The first group was

FIG. 1. *Trichophyton metagrophytes* recovered from a mouse injected intraperitoneally with a suspension of the sweepings of a vacuum cleaner used in a schoolhouse.

sacrificed a day after the inoculation and the rest of the groups, at weekly intervals until the fourth week. Peritoneal washings and slices of the liver and spleen of each sacrificed animal were inoculated in duplicates on Sabouraud's dextrose agar with penicillin, streptomycin and actidione. The frequency of recovery of the organism from the animals is presented in TABLE I. No gross lesion that could be attributed to the inoculated organisms was observed on the viscera of any of the animals.

The presence of dermatophytes in areas where people walk barefooted, such as swimming pool areas and public shower rooms, has long been suspected. In efforts to trace the source of infection and reinfection in tinea pedis, numerous attempts have been made to isolate the

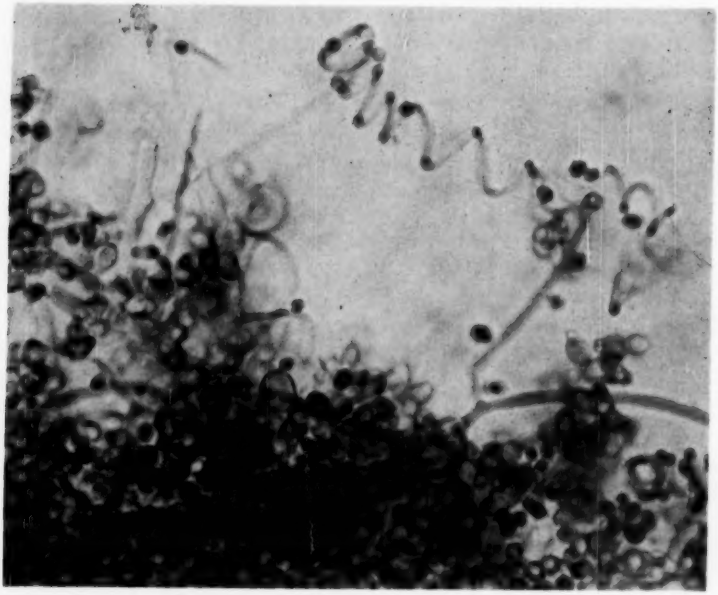

FIG. 2. Microscopic picture of a mount from the original isolate showing spirals and numerous microconidia.

dermatophytes from shoes and stockings and from places most likely to be contaminated. Aside from the reports of recovery of these fungi from used shoes and stockings (**2**, **3**, **6**), these systematic searches for dermatophytes in sites supposed to be harboring them met with relatively little success. *Trichophyton mentagrophytes* was recovered only

TABLE I

FREQUENCY OF RECOVERY OF *Trichophyton mentagrophytes* INJECTED INTRAPERITONEALLY INTO MICE

Period after injection	No. of mice injected	No. of mice with recovery of the organism		
		Peritoneal washings	Liver	Spleen
One day	5	5	4	5
One day	5	5	2	5
Two weeks	5	3	2	1
Three weeks	5	1	2	2
Four weeks	5	0	0	1

once from a bath mat by Gerencsér (**8**) and from a shower stall by Ajello and Getz (**2**). Lurie and Borok (**9**) recorded the accidental isolation of *Trichophyton mentagrophytes* from two samples of soil obtained from caves during their search for *Histoplasma capsulatum* to explain "cave disease" in a group of speleologists. They were also able to recover the organism from the viscera of mice inoculated intraperitoneally with the soil samples. Results recently obtained by Rosenthal *et al.* (**10**) indicate that pathogenic fungi are shed from the feet of individuals with tinea pedis and even those without clinical signs of the disease. This shedding of viable organisms from infected feet may account for their presence in the floor sweepings of a vacuum cleaner, as presently reported.

A major reason for the failure of the numerous attempts to recover the dermatophytes from exogenous sources and even from clinical materials is the over-growth of contaminants, particularly fungal. The incorporation of actidione in isolation media as recommended by Georg *et al.* (**7**) has been used to advantage in these investigations. Our report, as well as that of Lurie and Borok (**9**), suggests the feasibility of animal inoculation as an added procedure in the recovery of these dermatophytes from highly contaminated sources.

SUMMARY

A pathogenic strain of *Trichophyton mentagrophytes* was accidentally isolated from the sweepings of a vacuum cleaner used in a schoolhouse.

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NORTH AMERICAN ENTOMOGENOUS SPECIES OF CORDYCEPS[1]

E. B. Mains

(WITH 59 FIGURES)

The genus *Cordyceps* is most closely related to *Claviceps* and *Torrubiella*. It has commonly been placed in the Hypocreaceae of the Hypocreales and has been included by Lindau (**1897**) in the subfamily Clavicipiteae and by Seaver (**1911**) in the tribe Cordycipiteae. The Clavicipiteae form a well defined group and may properly be considered a family, Clavicipitaceae (Miller, **1949**; Diehl, **1950**). Both Miller and Diehl place it in the Sphaeriales. Filiform ascospores and usually capitate asci separate it from other families. The recognition of this group as an order, Clavicipitales by Nannfeldt (**1932**) does not appear justified. Diehl has proposed three subfamilies, placing *Cordyceps* with *Torrubiella*, *Ophiocordyceps* and *Poroniopsis* in the Cordycipitoideae.

The most comprehensive treatments of the genus have been by Saccardo (**1883**), Massee (**1895**) and Kobayasi (**1941**). Seaver (**1911**) has published concerning the genus for North America, including 18 species. Charles (**1941**) has included 39 species of *Cordyceps* in a check list of entomogenous fungi of North America. Of the 137 species given by Kobayasi 34 are reported for North America. There have been some differences in generic limitations. Massee excluded mycogenous species, suggesting that they be placed in a distinct genus *Cordylia*. Petch (**1931**) removed species having clavate asci and narrowly fusoid non-fragmenting ascospores to a genus *Ophiocordyceps*. Moureau (**1949**) has included the genus *Torrubiella*. The publication of the generic name *Cordyceps* has commonly been credited to Fries, Summa Veg. Scand. p. 381, 1849. Rogers (**1954**) has discussed the nomenclature, stating that the generic names *Cordylia* Fr. ex Ficinus & Schubert 1823 and *Cordyceps* Link 1833 were previously published for the genus but that *Cordylia* Fr. is a later homonym of *Cordylia* Pers. 1807, a genus of flowering plants. The genus as treated here is as follows:

[1] Paper from the Herbarium and Department of Botany of the University of Michigan. Published as excess pagination from funds of the Herbarium.

CORDYCEPS Link, Handbuch **3**: 347. 1833.

Sphaeria trib. *Cordyceps*, Fr. Syst. Myc. **2**: 325. 1823.

Cordylia Fr. ex Ficinus & Schubert, Fl. Dresden 2 ed. **2**: 331. 1823; non *Cordylia* Pers. 1807.

Torrubia Lév. ex Tul. Ann. Sci. Nat. III **20**: 43. 1853; non *Torrubia* Vell. 1825.

Akanthomyces Lebert, Zeit. wiss. Zool. **9**: 447. 1858.

Polistophtora Lebert, Zeit. wiss. Zool. **9**: 452. 1858.

Racemella Ces. Com. Soc. Crit. Ital. **1**(2): 65. 1861.

Ophiocordyceps Petch, Brit. Myc. Soc. Trans. **16**: 73. 1931. TYPE, *Cordyceps militaris*.

Stromata arising from dense masses of mycelia in insects, spiders or ascocarps of species of Elaphomyces, cylindric, clavate, capitate, simple or sometimes branched, whitish, yellow, orange, red, brown, ochraceous, grey, green or black, sometimes bicolored, stipitate, the stipes consisting of longitudinal, parallel or somewhat interwoven hyphae continuing above to form a central core in the upper perithecial portion or diverging and becoming more or less loosely interwoven; perithecia subgloboid, ovoid or conoid, with well developed walls, superficial, free or partly or completely embedded in a tissue of more or less loosely interwoven hyphae with or without a differentiated cortex or in a palisade-like tissue; asci cylindric, subfusoid or narrowly clavate, the walls very thin, usually thickened into caps at the apices; ascospores filiform or narrowly fusoid, hyaline, multiseptate, in many species breaking into 1-celled fragments at maturity; conidia 1-celled, hyaline, dry or glutinous, produced on the stromata, on synnemata of similar structure or on the mycelium.

The stromata, which arise from compact masses of mycelia (endosclerotia, pseudosclerotia) filling the hosts, differ considerably in size, color and shape. In some species they are very small, 1.5–2.5 mm (*C. thaxteri, C. clavulata*). In a number they reach a length of 10–13 cm or more (*C. sphecocephala, C. melolonthae*) and species having stromata 20 to 30 cm long have been described (*C. henleyae, C. gunnii*). There is often considerable variation in size within a species, due to differences in the depth of the host in the substratum, size of host and the number of stromata produced. Many of the species are known only from dried specimens and since color may be changed considerably on drying, specially pink and orange becoming light yellow or cream, the color of such species in the fresh condition may be different from that described. The stromata may be very long and slender, almost filiform (FIG. 21), acicular, cylindric, clavate (FIG. 17) or capitate having

cylindric, obovoid, ovoid, ellipsoid, globoid, flattened or peltate heads (FIGS. 31, 32).

The stromata are basically compact bundles of longitudinal parallel or somewhat interwoven hyphae. The perithecia develop upon the upper part in various ways. In one group they are superficial and free. They appear to be initiated beneath the outer longitudinal hyphae, breaking through early and becoming entirely superficial for the rest of their development as in *C. paludosa* (FIG. 2), or originating in or below a very thin layer of closely interwoven hyphae, emerging to become superficial, as in *C. superficialis* (FIG. 6). In another group the perithecia are in a tissue of loosely interwoven hyphae and may be partly embedded with the upper part of the perithecia projecting, as in *C. tuberculata* (FIG. 12), or may be completely embedded with only the ostiole opening to the outside (FIGS. 24, 38). In some of the latter the perithecia may appear to be projecting because of shrinkage of the soft tissue on drying, as in *C. militaris* (FIG. 18). The perithecia of some of the species of this group have been described as superficial. In some the hyphae may be more densely interwoven and darker in color toward the outside but there is no well differentiated cortex. In another group there is a well differentiated cortex. This may be a layer of pseudoparenchyma with or without an ectal layer one cell thick of hyaline oblong cells or a palisade-like layer of hyaline or brownish hyphae (FIGS. 35, 39). Jenkins's (**1934**) study of *C. capitata* (*C. agariciformia*) indicates that the cortex of this group is differentiated early in development of the stroma. In one species, *C. stylophora*, the cortex consists of parallel longitudinal hyphae which are continuations of the outer hyphae of the stipe (FIG. 52). Apparently the perithecia of this species originate deeper in the hyphal column than in *C. paludosa* and by their growth split off a cortical layer from the hyphae beneath. Only the necks of the perithecia finally penetrate through the cortical layer to the outside. The space between the perithecia becomes filled with loosely interwoven hyphae. Another species, *C. ravenelii*, shows a marked deviation. In this species the perithecia develop in a palisade-like layer of brown parallel hyphae extending outward at right angles to the longitudinal axis of the stroma (FIG. 54). Through the development of the perithecia, especially where crowded, this layer may be torn loose (FIG. 56) and sloughed off, leaving the perithecia superficial and free. Frequently the perithecia at maturity may be partly embedded and partly superficial and free.

The perithecia have well developed walls of pseudoparenchyma, in some species with two poorly differentiated layers. Jenkins states that

in *C. capitata* the wall of the perithecium develops from a spherical envelope of hyphae surrounding the ascogonium, some possibly originating from the ascogonium to form the inner wall. The perithecial layer may completely cover the upper portion of clavate or cylindric stromata (FIGS. 17, 53) or the heads of capitate stromata (FIGS. 15, 47, 48). It may surround the stroma leaving the apex sterile (FIG. 50) or may develop as lateral patches or cushions (FIGS. 40, 41, 42). In one species, *C. tuberculata,* the perithecia may develop on the mycelium or on a subiculum as well as on the upright stromata and sometimes specimens occur having perithecia only on the mycelium. In this latter condition the species has been described as a *Torrubiella.* It appears to be a species intermediate between the two genera. In most species the embedded perithecia are at right angles to the surface of the perithecial layer (FIGS. 18, 25) but in a few they are oblique (FIGS. 34, 38). In species with flattened or peltate heads they are vertical with the ostioles opening on the upper surface of the heads.

In most species the asci are long and narrow, in general cylindric (FIGS. 3, 19) but narrowing toward the bases and slightly at the apices. In *C. curculionum* they are 650–750 × 5–6μ. In some species, especially those having short and wide asci, they are clavate or fusoid (FIG. 4), in *C. clavata* (FIG. 16) being 80–110 × 8–12 μ. The walls of the asci are very thin in most species, thickening at the apex into hemispheric or subcylindric caps. Two species, *C. blattae* and *C. peltata,* have been described without caps. Their position in the genus and perhaps in the family is debatable.

The ascospores are hyaline, multiseptate, and in most species are filiform, nearly as long as the asci. At maturity the ascospores generally break into 1-celled cylindric or fusoid segments (FIGS. 7, 36). In a few species, specially those having short fusoid asci, the ascospores are narrowly fusoid and usually do not break into fragments. Whether paraphyses occur is doubtful. They have been described for a few species but may have been immature asci. Jenkins (**1934**) states that paraphysis-like hyphae occur in *C. capitata* which gelatinize and disappear. Periphyses lining the ostioles occur in a number of species.

Most of the reports of conidial stages for species of *Cordyceps* have been based on circumstantial evidence. Only a few species have been grown in culture and fewer have developed both ascogenous and conidial stages in culture (see Kobayasi, **1941**). The reports for some species have been assumptions based only on similar hosts. In most species the descriptions of conidial stages have been based on conidia produced on the stroma or conidial branches of the stromata (FIGS. 26, 51), on

associated synnemata or on the mycelium. Since stromata of *Cordyceps* are parasitized by other fungi, this probably has resulted in erroneous conclusions concerning some species. In most of the species for which conidial stages are known the conidia are produced on synnemata consisting of bundles of hyphae resembling the basic structure of the stromata. In the Fungi Imperfecti these are species of the Stilbaceae belonging to the genera *Isaria, Hirsutella, Hymenostilbe, Stilbum* and *Akanthomyces.* There is a number of unconnected entomogenous species of these genera that probably are conidial stages of *Cordyceps* (Mains, **1950, 1951b, 1955**). They differ mostly in whether the conidia are glutinous and adhere in clumps or globes of mucus, or dry and single or catenulate. The conidial stages of some species of *Cordyceps* are moniliaceous, belonging to species of *Spicaria, Sporotrichium* and *Cephalosporium.* These genera resemble the stilbaceous genera but lack synnemata, having the conidiophores produced on the mycelium. It seems probable that some species of *Cordyceps* may produce both stilbaceous and moniliaceous conditions.

Most of the species of *Cordyceps* are entomogenous. A few parasitize fungi; two described on sclerotia of *Claviceps* have not been reported from North America. A few closely related species on hypogeous fungi of the genus *Elaphomyces* have been discussed elsewhere (Mains, **1957**). Some occur on spiders (Mains, **1954**). Most of the species develop on the larvae, pupae or adults of insects. Kobayasi, in his summary of species for the world, gives 5 on Arachnida, 39 on Coleoptera, 36 on Lepidoptera, 20 on Hymenoptera, 12 on Hemiptera, 8 on Orthoptera, 3 on Diptera and 1 on Isoptera. As in other groups of parasitic fungi, host relationships have had an important part in classification, especially in the separation of species. Generally species have been limited to major groups of hosts and this is not always correlated with morphological differences. *C. myrmecophila* on ants and *C. sphecocephala* on wasps differ only slightly morphologically and they are on closely related groups of hosts. Their separation can logically be questioned. *C. lloydii* on ants and *C. dipterigena* on flies are very similar species with wider host differences. *C. bicephala* on ants, *C. nutans* on stink- and squash-bugs and *C. curculionum* on beetles are very closely related and Moureau (**1949**) has grouped them as varieties of *C. bicephala.* There is very little information available concerning the host ranges of species of *Cordyceps* based on inoculations. In this treatment although specific separations are not proposed based entirely on a host basis, established species with little or no morphologic differences are retained.

The North American species of *Cordyceps* according to host-groups are as follows:

Fungi. *Elaphomyces* spp. (see Mains, **1957**).

Arachnida (spiders). 6. *C. thaxteri*, 16. *C. grenadensis.*

Orthoptera (cockroaches, crickets). 36. *C. amazonica*, 38. *C. monticola.*

Homoptera (scale insects, cicadas). 10. *C. clavulata*, 18. *C. sobolifera*, 33. *C. hesleri.*

Coleoptera (beetles). 2. *C. acicularis*, 3. *C. superficialis*, 4. *C. michiganensis*, 8. *C. subsessilis*, 19. *C. martialis*, 20. *C. macularis*, 21. *C. melolonthae*, 23. *C. salebrosa*, 26. *C. curculionum*, 29. *C. variabilis*, 35. *C. entomorrhiza*, 37. *C. gracilis*, 39. *C. stylophora*, 40. *C. ravenelii*, 41. *C. peltata.*

Lepidoptera (butterflies, moths). 1. *C. paludosa*, 5. *C. crinalis*, 7. *C. tuberculata*, 11. *C. militaris*, 12. *C. washingtonensis*, 13. *C. elongata*, 17. *C. polyarthra*, 34. *C. belizensis*, 37. *C. gracilis.*

Diptera (flies). 24. *C. dipterigena.*

Hymenoptera (wasps, ants). 9. *C. langloisii*, 25. *C. lloydii*, 27. *C. sphecocephala*, 28. *C. myrmecophila*, 30. *C. unilateralis*, 31. *C. smithii.*

Unidentified hosts. 14. *C. olivascens*, 15. *C. caloceroides*, 22. *C. armeniaca*, 32. *C. insignis.*

The genus has been variously divided into subgenera. Tulasne (**1865**) under *Torrubia* separated the entomogenous species as *Torrubiae sinceriores* and the mycogenous species as *Cordyliae verae.* Lindau (**1897**) made a similar separation as *Eucordyceps* and *Cordylia.* Saccardo (**1883**) recognized *Cordylia* for the mycogenous species and divided the entomogenous species into those with "peritheciis stromate subimmersis," *Eucordyceps* and "peritheciis in stromate subsuperficialibus," *Racemella.* Schroeter (**1894**) recognized a subgenus *Racemella* for species with perithecia partly embedded and *Cordylia* for both entomogenous and mycogenous species having entirely embedded perithecia. Moureau (**1949**) has recognized three subgenera, *Torrubiella* in which he included species of the genus *Torrubiella, Eucordyceps* for species in which the ascospores break into fragments and *Ophiocordyceps* for those in which the ascospores do not fragment. Kobayasi (**1941**) has recognized three subgenera, *Ophiocordyceps* (genus *Ophiocordyceps* of Petch), *Neocordyceps* including species with oblique perithecia having curved necks and fusoid part spores, and *Eucordyceps* including species with perithecia at right angles to the surface or oblique with straight

necks and cylindric part spores. These subgenera are divided into 19 subtaxa.

The following subdivisions of the genus are proposed here.

I. Subg. RACEMELLA (Ces.) Sacc. Syll. Fung. **2**: 572. 1883.
Gen. *Racemella* Ces. Com. Soc. Crit. Ital. No. *2*: 65. 1861.

Asci with hemispheric or short cylindric caps; perithecia superficial and free. TYPE, *C. memorabilis* Ces.

Cesati included only one species in his genus *Racemella, R. memorabilis,* for which he described and illustrated free, superficial perithecia. Saccardo in addition to species with superficial perithecia also included species with partly embedded perithecia in the subgenus *Racemella.* As used here the subgenus is restricted to species with superficial free perithecia. The perithecia of the species of this subgenus originate either in a very thin outer layer of interwoven hyphae or among the outer longitudinal hyphae of the stromata and emerge very early and are free and superficial for the rest of their development (FIGS. 1, 2, 5, 6, 9, 11). It should be noted that because of shrinkage of a soft loose perithecial layer a number of species of the next subgenus have been described as having superficial, free perithecia. Species nos. 1–6 belong in this subgenus.

II. Subg. CORDYCEPS.

Asci with hemispheric or short cylindric caps; perithecia partly or completely embedded in a tissue consisting of more or less loosely interwoven hyphae with or without a differentiated cortex. TYPE, *C. militaris.*

This subgenus includes most of the species, nos. 7–39. The following four sections are recognized.

1. Sect. **Hemicordyceps** sect. nov.

Peritheciis semiimmersis in rectis stromatibus quoque in mycelis. TYPE, *C. tuberculata.*

This section contains one very variable species, no. 7, *C. tuberculata.* The perithecia are partly embedded in a soft tissue consisting of loosely interwoven hyphae and are produced both on upright stromata and on the mycelium. In the latter condition it resembles species of *Torrubiella.* It is intermediate between *Cordyceps* and *Torrubiella.*

2. Sect. CORDYCEPS.

Perithecia in upright stromata, not produced on the mycelia, partly or completely embedded in a tissue of loosely interwoven hyphae without a differentiated cortex. TYPE, *C. militaris*.

In species of this section the perithecia may become more prominent from shrinkage of the soft perithecial layer, sometimes appearing superficial. Species Nos. 8–21 belong here.

3. Sect. CREMASTOCARPON Kobayasi, Sci. Rep. Tokyo. Bun. Daig. **5**: 174. 1941.

Perithecia in upright stromata, not produced on the mycelia, completely embedded in a tissue having a differentiated cortex of pseudoparenchyma with or without a palisade-like ectal layer. TYPE, *C. nutans*.

Kobayasi proposed the name for a section restricted to species with obliquely embedded perithecia. As used here it applies to all species with a differentiated cortex of pseudoparenchyma with or without an ectal layer. Two subsections are recognized as follows.

3a. Subsect. **Mycogenae** subsect. nov.

Parasiticae in hypogaeis fungis. TYPE, *C. ophioglossoides*.

These species are parasites of species of *Elaphomyces* and have been discussed elsewhere (Mains **1957**).

3b. Subsect. **Entomogenae** subsect. nov.

Parasiticae in insectis. TYPE, *C. nutans*.

This subsection includes species Nos. 22–38 with insects as hosts.

4. Sect. **Cystocordyceps** sect. nov.

Peritheciis in rectis stromatibus immersis, non in myceliis; corticibus elongitudinalibus hyphis. TYPE, *C. stylophora*.

In the one species No. 39 the cortex of the perithecial layer consists of longitudinal parallel hyphae which are a continuation of the outer hyphae of the stipe (FIG. 52). The space below the cortex and between the perithecia is filled with loosely interwoven hyphae.

III. Subg. **Cryptocordyceps** subgen. nov.

Ascis capitatis; peritheciis stromate paliforme immersis. TYPE, *C. ravenelii*.

In the one species No. 40, the perithecia develop in a palisade-like layer consisting of brown more or less parallel hyphae at right angles

to the surface (FIG. 54). They may partly emerge (FIG. 55) or may push the layer off (FIG. 56) and become free.

IV. Subg. OPHIOCORDYCEPS (Petch) Kobayasi, Sci. Rep. Tokyo Bun. Daig. **5**: 68. 1941.

Gen. *Ophiocordyceps* Petch, Brit. Myc. Soc. Trans. **16**: 73. 1931.

Asci not capitate. TYPE, *C. blattae*.

As treated by Petch, Kobayasi and Moureau, *Ophiocordyceps* includes species having clavate asci with or without caps and narrowly fusoid ascospores which do not fragment at maturity. In this treatment the subgenus is restricted to species with non-capitate asci. This is a character which is not only unique for the genus but also for the family and the relationships of the species are somewhat questionable. Two species *C. blattae* and *C. peltata* belong here. Of these the latter, No. 41 has been reported for North America.

In addition to specimens in the Herbarium of the University of Michigan (MICH) the specimens of the genus from the Mycological Collections of the United States Bureau of Plant Industry (BPI), the Herbarium of the Department of Plant Pathology of Cornell University (CUP), the Farlow Herbarium, Harvard University (FH) and the Herbarium of the New York Botanical Garden (NY) have been available for this study.

KEY TO THE SPECIES

A. Hosts fungi, *Elaphomyces* spp. . . . . (Mains **1957**)
A. Hosts spiders and insects . . . . . B
B. Asci with walls thickened into apical caps C
B. Asci without apical caps; on coleopterous larvae . . . . . 41. *C. peltata*
C. Perithecia superficial and free . . . . . D
C. Perithecia partly or completely embedded I
D. Stromata very small, 1.5–2.5 mm long; perithecia 1–4; on spiders . . . . . 6. *C. thaxteri*
D. Stromata larger, 1–10 cm long; perithecia numerous . . . . . E
E. Perithecia large, 800–855 × 375–410 μ; asci 480–550 × 8–10 μ; on lepidopterous larvae . . . . . 1. *C. paludosa*
E. Perithecia and asci smaller . . . . . F
F. Stromata long, 6–10 cm; on coleopterous larvae . . . . . 2. *C. acicularis*
F. Stromata shorter, 5 cm or less . . . . . G
G. Perithecia chocolate-brown, the walls thick, very rough; on coleopterous larvae . . . . . 3. *C. superficialis*
G. Perithecia grayish brown or ochraceous orange, the walls thin, smooth . . . . . H
H. Stromata 1.5–2.5 cm long, ochraceous to ochraceous orange; asci cylindric; on coleopterous larvae . . . . . 4. *C. michiganensis*
H. Stromata up to 5 cm long, grayish brown; asci fusoid; on lepidopterous larvae . . . . . 5. *C. crinalis*

I. Perithecia produced in a palisade-like layer of parallel brown hyphae (FIG. 54), some finally becoming free by sloughing off of the layer; on coleopterous larvae ..... 40. *C. ravenelii*

I. Perithecia produced in a layer of interwoven hyphae with or without a differentiated cortex ..... J

J. Perithecia vertically embedded in the apex of a short cylindric stroma (FIG. 13) ..... 8. *C. subsessilis*

J. Perithecia distributed otherwise ..... K

K. Perithecia opening on the upper surface of a flattened head (FIGS. 14, 30, 32) L

K. Perithecia in a layer covering heads or upper portions of stromata or in lateral cushions or patches ..... Q

L. Asci short, 250 μ or less ..... M

L. Asci longer, 480 μ or more ..... O

M. Perithecia embedded in a layer of loosely interwoven hyphae without a cortex; on larvae of mason wasps ..... 9. *C. langloisii*

M. Perithecia embedded in a layer with a differentiated cortex ..... N

N. Heads brownish black, very rough; cortex of brown pseudoparenchyma; perithecia 270–400 × 130–180 μ; on ants (*C. formicivora*) ..... 30. *C. unilateralis*

N. Heads reddish brown, smooth; cortex having a palisade-like ectal layer of parallel hyaline hyphae; perithecia 450–650 × 220–250 μ; on an unidentified host ..... 22. *C. armeniaca*

O. Stromata bicolored; heads and upper portion of stipes cream colored when dried, red fresh, lower portions of stipes brownish black; on adult beetles ..... 23. *C. salebrosa*

O. Stromata not distinctly bicolored ..... P

P. On flies ..... 24. *C. dipterigena*

P. On ants ..... 25. *C. lloydii*

Q. Perithecia embedded obliquely to the surface of the perithecial layer ..... R

Q. Perithecia embedded at right angles to the surface of the perithecial layer ..... U

R. Perithecia in a layer covering the upper portion of a cylindric to clavate stroma; on coleopterous larvae ..... 19. *C. martialis*

R. Perithecia in ovoid heads ..... S

S. Stromata bicolored, heads and upper portions of stipes cream to brownish yellow dried, pink or red fresh, lower portion of stipe black; on adult beetles ..... 26. *C. curculionum*

S. Stromata not distinctly bicolored ..... T

T. Head with a central core of longitudinal hyphae; ectal layer of head 1 cell thick of oblong cells; on wasps ..... 27. *C. sphecocephala*

T. Head without a central core; ectal layer of the head a palisade of parallel septate hyphae; on ants ..... 28. *C. myrmecophila*

U. Stromata on adult moths; perithecia sometimes developing from mycelium covering the host ..... 7. *C. tuberculata*

U. Stromata on other insects or if on moths from the larvae or pupae; perithecia not developing from the mycelium V

V. Apex of stroma sterile; perithecial layer surrounding the stroma below or in lateral cushions or irregular patches ..... W

V. Apex of stroma fertile; perithecial layer covering heads or the upper part of a cylindric or clavate stroma ..... AA

W. Perithecia in a cylindric layer surrounding the stem; cortex of longitudinal parallel hyphae; on coleopterous larvae ..... 39. *C. stylophora*
W. Perithecia in lateral cushions or patches; cortex lacking or not as above X
X. Stromata large, 3–13 cm long, 5–15 mm thick; perithecia in large irregular lateral patches; on coleopterous larvae ..... 21. *C. melolonthae*
X. Stromata smaller, less than 3.5 cm long, 1 mm thick; perithecia in small lateral cushions ..... Y
Y. Stromata ochraceous or ochraceous orange; perithecia 330–600 × 230–400; asci cylindric, 200–350 × 8–10 μ; on coleopterous larvae ..... 29. *C. variabilis*
Y. Stromata ochraceous salmon, vinaceous fawn, dark brown or brownish black; perithecia and asci smaller ..... Z
Z. Stromata ochraceous salmon to vinaceous fawn; on coleopterous larvae ..... 20. *C. macularis*
Z. Stromata light brown to brownish black; on ants ..... 30. *C. unilateralis*
AA. Perithecia partly or completely embedded in a layer of loosely interwoven hyphae without a cortex ..... BB
AA. Perithecia in a layer of loosely interwoven hyphae with a differentiated cortex ..... KK
BB. Stromata green ..... 14. *C. olivascens*
BB. Stromata yellow, orange, red, reddish brown, gray or brownish black CC
CC. Stromata very small, 2–4 mm long; asci clavate or subfusoid, 80–110 × 8–12 μ; on scale insects ..... 10. *C. clavulata*
CC. Stromata and asci larger; on other insects ..... DD
DD. On cicadas; stromata often with conidial branches on the stipes ..... 18. *C. sobolifera*
DD. On spiders or lepidopterous or coleopterous larvae; stromata without conidial branches ..... EE
EE. Asci 300 μ or less in length ..... FF
EE. Asci more than 300 μ long ..... JJ
FF. Stromata robust, 3–8 mm thick; on coleopterous larvae ..... 21. *C. melolonthae* var. *rickii*
FF. Stromata slender, 2 mm or less thick ..... GG
GG. Perithecia small, 200–250 × 85–150 μ; on spiders ? ..... 15. *C. caloceroides*
GG. Perithecia larger ..... HH
HH. Stromata red, subcapitate; on spiders ..... 16. *C. grenadensis*
HH. Stromata yellow or yellowish brown, clavate or cylindric; on lepidopterous larvae II
II. Stromata caespitose, clavate ..... 17. *C. polyarthra*
II. Stromata 1 or 2, cylindric, with acute apices ..... 13. *C. elongata*
JJ. Stromata orange buff to mikado orange; asci cylindric; ascospores breaking into small segments; on lepidopterous larvae ..... 11. *C. militaris*
JJ. Stromata sulphur or pinard yellow; asci clavate; ascospores not breaking into fragments; on lepidopterous larvae ..... 12. *C. washingtonensis*
KK. Asci clavate, 90–120 × 8–9 μ; on wasps ..... 31. *C. smithii*
KK. Asci larger LL
LL. Stromata clavate or subcapitate ..... MM
LL. Stromata capitate ..... NN
MM. Asci 600–700 × 5–6 μ; cortex with a palisade-like ectal layer of parallel hyphae; on an unidentified host ..... 32. *C. insignis*

MM. Asci 300–360 × 6–7 μ; cortex without a differentiated ectal layer; on cicadas ..... 33. *C. hesleri*
NN. Cortex of pseudoparenchyma with an ectal layer of oblong cells or a palisade of parallel hyphae ..... OO
NN. Cortex of pseudoparenchyma without an differentiated ectal layer; on lepidopterous larvae ..... 34. *C. belizensis*
OO. Ectal layer of cortex 1 cell thick of oblong cells; on coleopterous larvae ..... 35. *C. entomorrhiza*
OO. Ectal layer of the cortex a palisade of parallel septate hyphae ..... PP
PP. Asci 180–210 × 4 μ; on cockroaches and locusts ..... 36. *C. amazonica*
PP. Asci more than 400 μ long ..... QQ
QQ. Stromata with heads ochraceous to mahogany red; the stipes chrome to straw yellow; on lepidopterous and coleopterous larvae ..... 37. *C. gracilis*
QQ. Stromata with heads brownish gray; the stipes light gray; on mole crickets ..... 38. *C. monticola*

I. SUBGENUS RACEMELLA

1. CORDYCEPS PALUDOSA Mains, Papers Mich. Acad. Sci. **25**: 83. 1940. (FIGS. 1–3).

Stromata single or occasionally 2 or 3 from host, very slender, acicular, attenuated to hair like apices, 5.5–13 cm long, 0.5–1.0 mm thick, gray or brownish gray, tomentose below, consisting of hyaline narrow compact longitudinal hyphae within, with an outer brown layer of longitudinal hyphae having smaller cells, below on the stipe having a covering of very loosely outwardly interwoven hyphae sometimes tufted; perithecia narrowly ovoid to conoid, 800–855 × 375–410 μ, grayish brown below, deep brown above, with a wall up to 50 μ thick of two layers, the inner of very narrow hyaline longitudinal hyphae ending around the ostiole in terminal enlarged cells, the outer of wider, brownish to brown, densely to loosely interwoven hyphae; asci cylindric, 480–550 × 8–10 μ, with a 4 μ thick cap; ascospores filiform, hyaline, multiseptate, nearly as long as the ascus, the cells 12–18 × 2–2.5 μ, not breaking into segments.

On larvae of Lepidoptera. Kent Lake, Oakland County, Michigan, *A. H. Smith 7559*, TYPE, *9640* (MICH).

The perithecia of this species appear to originate within the outer brown layer of the stroma, early breaking through and becoming superficial (FIGS. 1–2). The long filiform ascospores do not break into segments. This is a character stressed as diagnostic for *Ophiocordyceps* but *C. paludosa* (FIG. 3) does not have the short fusoid asci given for that taxon. It approaches *C. superficialis* in color and differs from both *C. superficialis* and *C. michiganensis* in larger stromata and much larger perithecia and asci.

2. CORDYCEPS ACICULARIS Rav. ex Berk. Jour. Linn. Soc. **1**: 158. 1857. (FIG. 4).

Cordyceps carolinensis Berk. & Rav. nom. nudum, Rav. Fung. Car. fasc. 4: 29. 1855.

Ophiocordyceps acicularis Petch, Brit. Myc. Soc. Trans. **18**: 60. 1933.

Stromata slender, cylindric, 6–10 cm long, 0.5–1 mm thick, ochraceous, warm buff or grayish brown, consisting of compact longitudinal parallel hyphae, hyaline within, brownish to dark brown toward the surface, with a very thin ectal layer of interwoven hyphae between the bases of the perithecia; perithecia subgloboid to broadly ovoid, 250–400 × 200–300 μ, ochraceous to dark brown, with the wall up to 50 μ thick, mostly of small hyaline thin-walled cells with outer cells larger and brown, superficial, free, scattered to crowded on the upper part of the stroma; asci somewhat fusoid, 200–250 × 8–12 μ, narrowed to 4–5 μ at the apices, with 4 μ thick cap; ascospores filiform, 160–200 × 1.5–2.5 μ, multiseptate, cells up to 6 μ long.

On larvae of Coleoptera. Laurel Run, Pennsylvania, *B. B. and L. O. Overholts 20215* (BPI). South Carolina, *H. W. Ravenel 1276*, TYPE, Curtis Coll. (FH).

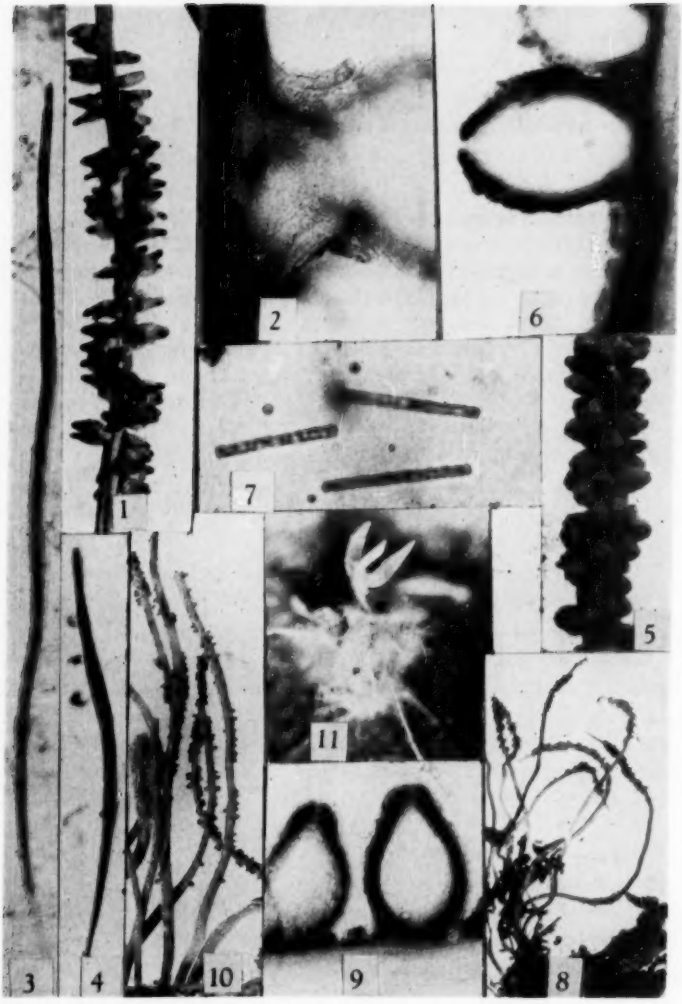
There has been considerable uncertainty concerning the identity of this species. It was described by Berkeley in the same article with *C. ravenelii*, to which it was considered closely related. Petch (**1933**) has considered them the same. Berkeley cites Rav. No. 1276 in his description of the species and there is a Ravenel specimen bearing this number in the Curtis Collection of the Farlow Herbarium. There is also a collection (Curtis 3080, Ravenel 1272) which is cited by Berkeley in his description of *C. ravenelii*. The two are different species (compare *C. ravenelii*).

Cordyceps carolinensis was issued by Ravenel in his Fungi Car. 4: 29 without a description. Specimens of this number have been seen from three herbaria and all have been sterile. They appear to be *C. acicularis*. There are also sterile specimens from Connecticut, Maine and Ontario in the Farlow Herbarium which are probably this species.

3. CORDYCEPS SUPERFICIALIS (Peck) Sacc. Syll. Fung. **2**: 574. 1883. (FIGS. 5–7).

Torrubia superficialis Peck, N. Y. State Botanist Rep. **28**: 70. 1876.

Stromata very slender with acuminate apices, 1–5 cm long, 0.3–2.0 mm thick, light gray, grayish brown or black with age, consisting of



FIGS. 1–3, *C. paludosa*, type; 1, portion of stroma with perithecia, × 6; 2, base of perithecium and ruptured outer hyphae of stroma, × 120; 3, ascus, × 300. FIG. 4, *C. acicularis*, ascus, × 300. FIGS. 5–7, *C. superficialis;* 5, portion of stroma with perithecium, × 10; 6, perithecia, × 75; 7, part-spores, × 1000. FIGS. 8–9, *C. michiganensis*, type; 8, stromata, × 2; 9, perithecia, × 75. FIG. 10, *C. crinalis*, type, stromata, × 5. FIG. 11, *C. thaxteri*, type, stroma, × 10.

compact parallel longtudinal hyphae dark brown within, brownish to hyaline below the surface, with a thin (20–50 μ) ectal layer of hyaline interwoven hyphae; perithecia broadly ovoid to subgloboid, 320–560 × 250–420 μ, chocolate-brown, rough, the wall thick, up to 90 μ with an inner layer of thin hyaline cells, the outer mostly of large (20 μ) angular or globoid cells; asci cylindric, 170–360 × 6–9 μ, with a 2 μ thick cap; ascospores filiform, multiseptate breaking into 1-celled fragments 14–32 × 1.5–2 μ.

On larvae of Coleoptera. Connecticut, *R. Thaxter,* FH 6130. Massachusetts, *G. D. Darker 5355* (Reliq. Farl. 704), *4860* (FH, NY, BPI). Michigan, *A. H. Smith 15130* (MICH). New Hampshire, *R. Thaxter,* FH 4030. New York, *Chas. H. Peck,* TYPE (NYS). North Carolina, *A. H. Smith 10395* (MICH), *L. R. Hesler 14362* (MICH), *Hesler & Boarts 15759* (CUP). Tennessee, *A. H. Smith 10401* (MICH). Ontario, *H. S. Jackson 5043* (MICH).

This species has been treated as a synonym of *C. acicularis* and it occurs in herbaria under that name. The perithecia are distinctive (FIGS. 5, 6). They appear to originate within the outer longitudinal hyphae of the stroma, splitting it and emerging to become superficial and free. There is, however, a thin layer of closely outwardly interwoven hyphae between the bases of the perithecia (FIG. 6). The walls of the perithecia are very thick and are irregularly split, resulting in a very irregular rough surface.

4. CORDYCEPS MICHIGANENSIS Mains, Am. Phil. Soc. Proc. **74**: 266. 1934. (FIGS. 8, 9).

Stromata single or commonly in groups of 3 to 11, slender, acuminate, 1.5–2.5 cm long, 0.2–0.4 mm thick, ochraceous, ochraceous buff or ochraceous orange, minutely furfuraceous, consisting of narrow compact parallel longitudinal hyphae, with a thin, 25–30 μ, outer layer of more or less densely interwoven short hyphae broken up into scales on the stipe; perithecia broadly ovoid, 240–430 × 210–350 μ, ochraceous orange, smooth, the wall 25–50 μ thick of closely interwoven hyphae becoming longitudinal and parallel around the ostiole, superficial, scattered or crowded on the upper part of the stroma; asci cylindric, 130–250 × 4–6 μ, with a 3–4 μ thick cap; ascospores filiform, multiseptate, tardily breaking into 1-celled fragments, 12–50 × 1–1.5 μ.

On larvae of Coleoptera. Michigan, *E. B. Mains 32–148, 33–403; E. B. & E. E. Mains 32–391,* TYPE; *E. B. Mains & A. H. Smith 33–379, 5326; A. H. Smith 1432, 6306, 6684, 21791, 25648, 36909; M. Lange; H. A. Imshaug 2905, 3126* (all MICH). North Carolina, *R. Thaxter,*

FH 6140; *A. H. Smith 9667, 10397* (MICH). Ontario, *A. H. Smith 4508* (MICH).

This species is usually found on beetle larvae in rotten logs. It appears to be similar to *C. memorabilis* as described by Cesati from Italy, which apparently is not otherwise known.

5. CORDYCEPS CRINALIS Ellis ex Lloyd, Myc. Writ. **6**: 912. 1920. (FIG. 10).

Stromata numerous, "about 30," slender, 5 cm long, 0.2–0.3 mm thick, simple or occasionally furcate above, light grayish brown, consisting of longitudinal somewhat interwoven hyaline hyphae within and nearly parallel brown hyphae to the outside; perithecia narrowly ovoid, 300–360 × 175–240 μ, light reddish brown, smooth, the wall 30–40 μ thick, of hyaline narrow cells within, of light brown nearly globoid cells in an outer layer, superficial, free, scattered or crowded; asci somewhat fusoid, 150–185 × 6–9 μ, with a 3–4 μ thick cap; ascospores filiform, nearly as long as the asci, 1.5 μ thick, the septation obscure.

On larva of a Lepidoptera. Newfield, New Jersey, Aug. 7, 1887, *Ellis,* TYPE (NY).

This species is known only from the type. As has been discussed elsewhere (Mains **1940c**) it was reported by Ellis and Everhart as *Cordyceps sphingum.* Lloyd concluded that it was a valid species, for which he proposed a manuscript name of Ellis's. It is closely related to *C. acicularis,* differing in shorter cespitose stromata, smaller and less fusoid asci and lepidopterous host.

6. CORDYCEPS THAXTERI Mains, Jour. Elisha Mitchell Sci. Soc. **55**: 120. 1939. (FIG. 11).

Stromata small, cylindric, 1.5–2.5 mm long, 0.15–0.18 mm thick, enlarged 0.18–0.3 mm at apices, brownish, villose, composed of compact longitudinal somewhat interwoven hyphae; perithecia narrowly ovoid or conoid, 960–1200 × 300–360 μ, few, 1–4, superficial, free, villose; asci cylindric, 600–780 × 6–7 μ, with a 4 μ thick cap; ascospores filiform, multiseptate, 1–1.5 μ thick, the cells 6–10 μ long, tardily breaking into 1-celled fragments.

Conidial stage: *Akanthomyces arancarum* (Petch) Mains, Mycologia **42**: 574. 1950. Synnemata similar to the stromata, white pulverulent from the conidia; phialides somewhat scattered, forming a loose hymenium, obovoid or ellipsoid, 6–12 × 4–8 μ, abruptly narrowed above into short sterigmata; conidia narrowly obclavate, 8–14 × 1.5–3 μ, hyaline, catenulate.

On spiders, Arachnida. Maine, *R. Thaxter,* FH 6258, FH 649. North Carolina, *R. Thaxter,* FH 665, FH 4123 (TYPE), FH 4122A.

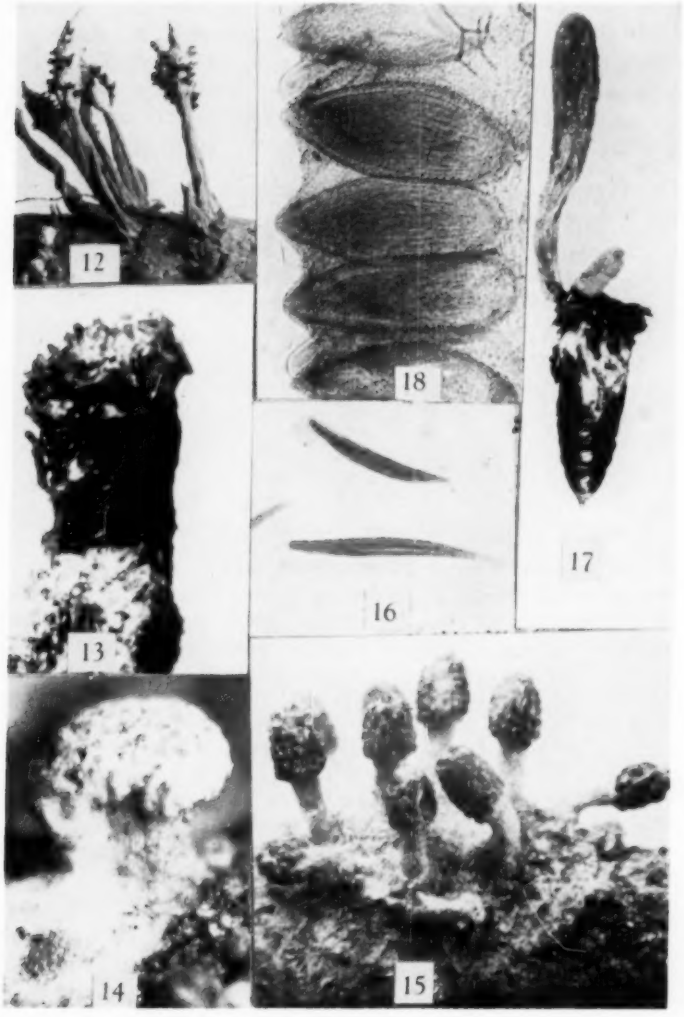


FIG. 12, *C. tuberculata*, stromata, × 3. FIG. 13, *C. subsessilis*, stroma with vertical perithecia, × 16. FIG. 14, *C. langloisii*, type, capitate stroma, × 16. FIGS. 15–16, *C. clavulata;* 15, stromata on scale-insect, × 6; 16, asci, × 300. FIGS. 17–18, *C. militaris;* 17, pupa and stroma, × 1.5; 18, perithecia, × 100.

The small size of the stroma, and the few, large perithecia make this a unique species (FIG. 11). There is some indication of a tendency to the development of a perithecial layer in the villose condition of the stromata and perithecia, which, however, are free and superficial.

II. SUBGENUS CORDYCEPS. SECTION 1. HEMICORDYCEPS

7. CORDYCEPS TUBERCULATA (Lebert) Maire, Bul. Soc. Hist. Nat. Afrique Nord. **8**: 165. 1917. (FIG. 12).
Akrophyton tuberculatum Lebert, Zeitschr. wiss. Zool. **9**: 448. 1858.
Torrubia sphingum Tul. Sel. Fung. Carp. **3**: 12. 1865.
Cordyceps sphingum Berk. & Curt. Jour. Linn. Soc. **10**: 375. 1869.
Ophionectria cockerellii Ellis, Jour. Inst. Jamaica **1**: 142. 1892.
Cordyceps cockerellii Ellis, Jour. Inst. Jamaica **1**: 180. 1892.
Cordyceps isarioides Curt. ex Massee, Ann. Bot. **9**: 36. 1895.
Cordyceps moelleri Henn. Hedwigia **36**: 221. 1897.
Cordyceps cristata Moeller, Phyc. u. Asco. 212. 1901.
Cordyceps rostrata Henn. Hedwigia **41**: 167. 1902.
Cordyceps tarapotensis Henn. Hedwigia **43**: 246. 1904.
Torrubiella ochracea Pat. Bull. Soc. Myc. France **22**: 58. 1906.

White mycelia covering adult moths, often attaching them to the substrata; stromata several to many from various parts of the host, sometimes lacking, very variable, short cylindric, long cylindric, clavate, acute or acuminate, 2–11 mm long, 1.5–2.0 mm thick above, yellowish white or gray above, with a central core of compact longitudinal somewhat interwoven or parallel brown hyphae, with brown, 0.5–1.0 mm thick stipes having a thin layer of hyaline or brownish loosely interwoven hyphae covering the central core; perithecia narrowly ovoid or conoid, 420–900 × 180–370 μ, dark brown, crowded in groups or scattered, partly embedded in a soft cottony layer covering the upper part of the stroma, consisting of loosely interwoven hyphae, sometimes becoming more or less superficial by shrinkage of the stroma, sometimes developing more or less superficially on the mycelium; asci cylindric, 360–600 × 4–5 μ, with a 4 μ thick cap; ascospores filiform, multiseptate, breaking into 1-celled fragments, 2–6 × 0.5–1 μ.

On adult moths, Lepidoptera, Sphingidae, Coccytius. North Carolina, *R. Thaxter*, FH 4053, FH 4054; Curtis Coll. (*C. isarioides*), FH. Cuba, *C. Wright 732*, Fungi Cub. 746 (as *C. sphingum*). Dominican Republic, *H. A. Allard* (BPI). Jamaica, *A. S. Hitchcock* (FH); *A. H. Ritchie*, Lloyd H41285 (BPI); *Mrs. Swanson* (*C. cockerellii* Ellis Coll., NY). Panama, *Bernard Lowy*. British Honduras, *W. A. Schipp* (MICH).

This species is frequently treated as *Cordyceps sphingum*, a name based on *Isaria sphingum* Schw., a conidial condition of doubtful connection (Mains, **1950**). It is frequently collected in a sterile condition and there are collections from Alabama, Connecticut, Massachusetts, New Hampshire, and Tennessee which are probably this species. It is a variable species and its several variants have been described as a number of species (Petch, **1932**; Kobayasi, **1941**). Not only are the perithecia produced on stromata but they may develop more or less superficially on the mycelium which covers the host. The stromata vary from slight cylindric or hemispherical protuberances to fairly well developed clavae (FIG. 12). The perithecia are partly embedded in the soft perithecial layer, usually one-third to one-half projecting. Through shrinkage or weathering the layer may mostly or entirely disappear, the perithecia then appearing superficial. There is a specimen labeled *Cordyceps isarioides* M.A.C., Julio 1866, Hillsboro, N. C., in the Curtis Collection of the Farlow Herbarium in which the perithecia are superficial on stromata and on the mycelium covering the host. It seems probable that this is part of the collection sent by Curtis to Berkeley to which Massee refers in the publication of *C. isarioides*. As Petch (**1932**) has concluded, it is *C. tuberculata*. Occasionally perithecia may be produced only on the mycelium without the production of stromata. In this condition the fungus has been described as species of *Ophionectria* and *Torrubiella* (*Ophionectria cockerellii*, *Torrubiella ochracea* Pat.). Moureau (**1949**) states that this species develops very slowly over several months and is very sensitive to environmental conditions, which may result in stopping the development at different stages.

Akanthomyces aculeata (*Hymenostilbe sphingum*) has been reported (Petch, **1932**, **1944**) to be the conidial stage of *C. tuberculata*. There is a collection, FH 6125 from Trinidad, in the Farlow Herbarium which has synnemata of *Insecticola pistillariaeformis* (Pat.) Mains and perithecia of *C. tuberculata* together. The specimen is in the *Torrubiella* condition with the perithecia on the mycelium. *I. pistillariaeformis* may therefore be the conidial stage of *C. tuberculata* or it is also possible that two species may be involved, distinguished by different conidial stages.

II. SUBGENUS CORDYCEPS. SECTION 2. CORDYCEPS

8. CORDYCEPS SUBSESSILIS Petch, Brit. Myc. Soc. Trans. **21**: 39. 1937. (FIG. 13).

Stromata poorly developed, irregularly cylindric, 4.5–10 mm long, 1–5 mm thick, mostly buried in the substratum with only the apices pro-

jecting, yellowish to brownish, consisting of compact longitudinal somewhat interwoven hyaline hyphae; perithecia narrowly ovoid to conoid, 800–1080 × 324–444 μ, brown, with the walls well differentiated, vertically embedded in clusters in the apices of the stromata, at first entirely embedded and covered with loosely interwoven hyphae, finally more or less projecting from the shrinkage of the tissue; asci cylindric, 430–600 × 3–4 μ, with a 2 μ thick cap; ascospores filiform, multiseptate, breaking into 1-celled part-spores, 3–6 × 0.5–1 μ.

On larvae of Coleoptera. Michigan, *A. H. Smith 7724* (MICH). North Carolina, *R. Thaxter*, FH 6155. Tennessee, *R. Thaxter*, FH 6145, TYPE. Washington, *A. H. Smith 14573* (MICH).

This species has poorly developed stromata. Petch was uncertain whether it should be referred to *Cordyceps* or *Torrubiella*. The perithecia are not superficial on a mycelium or on a byssoid flat, thin stroma as in *Torrubiella*. They are produced vertically in the apices of the stromata and do not form a well developed head (FIG. 13). They are not superficial and free as described by Petch but are in a soft loose tissue. Through shrinkage of the tissue they may more or less appear superficial.

9. CORDYCEPS LANGLOISII Ellis & Everh. N. Am. Pyrenomycetes 62. 1892. (FIG. 14).

Stromata capitate, small, 1.5–3 mm long, with the heads flattened, 1.2–2 mm wide, 0.3 mm thick, yellowish to reddish purple, punctate on the upper surface by the ostioles, with the stipes very short, 0.5–0.6 mm thick, composed of longitudinal parallel hyphae; perithecia narrowly ovoid, 260–400 × 100–230 μ, vertical with ostioles opening on the upper surface of the head, with the wall 4–6 μ thick, completely embedded in a tissue composed of loosely interwoven narrow hyphae without a differentiated cortex; asci cylindric, 125–200 × 2–3.5 μ, with a 1.5–2 μ thick cap; ascospores filiform, 0.5 μ thick, multiseptate, part-spores not seen.

On larvae of "mason wasp," Hymenoptera. Louisiana, *A. B. Langlois 2295*, TYPE (NY).

There has been considerable uncertainty concerning the identity of this species. Lloyd (**1920**) and Petch (**1933**) have considered it to be conspecific with *C. armeniaca*. A study of the type of *C. armeniaca* in the Curtis Collection of the Farlow Herbarium has shown that they are distinct species. *C. armeniaca* has the perithecia in a layer over the entire surface of the head, which has a differentiated cortex. The specimen collected by D. H. Linder, No. 600 on mud wasp nest, Bartica, British Guiana (FH) reported by Petch (**1939**) as *C. armeniaca* is

C. langloisii. Petch (**1933**) also has considered that *C. langloisii* is the same as *C. dittmari* Quélet. However, the illustration given by Quélet (**1877**) shows that the later species has a spherical head with the ostioles opening over the entire surface.

10. CORDYCEPS CLAVULATA (Schw.) Ellis & Everh. N. Am. Pyrenomycetes 61. 1892. (FIGS. 15, 16).

Sphaeria clavulata Schw. Trans. Am. Phil. Soc. II. **4**: 188. 1832.
Cordyceps pistillariaeformis Berk. & Br. Ann. Mag. Nat. Hist. **7**: 451. 1861.
Torrubia pistillariaeformis Cooke, Handb. Brit. Fungi **2**: 771. 1871.
Torrubia clavulata Peck, Rep. N. Y. State Botanist **28**: 70. 1876.
Ophiocordyceps clavulata Petch, Brit. Myc. Soc. Trans. **18**: 53. 1933.

Stromata several to many, subcapitate or clavate, small, 2–4 mm long, with heads cylindric or ovoid, 1–1.5 × 0.5–1 mm, brownish black, verrucose from the crowded perithecia, with stipes 0.3–0.5 mm thick, gray or brownish gray, matted tomentous, with central core of compact longitudinal somewhat interwoven brownish to brown hyphae, with outer hyphae of stipe hyaline, loosely interwoven; perithecia ovoid, 150–250 × 110–150 μ, with wall light brown, poorly differentiated below, dark brown to chocolate and well differentiated above, crowded, embedded except for the apices at right angles to the surface in a soft layer consisting of loosely interwoven brownish hyphae sometimes dark brown at the surface but without a well differentiated cortex; asci clavate or subfusoid, 80–110 × 8–12 μ, with a 2–3 μ thick cap; ascospores narrowly clavate, 42–80 × 2.5–3.5 μ, multiseptate, with cells 4–6.5 μ long, not breaking into part-spores.

Conidial stage: *Hymenostilbe lecaniicola* (Jaap) Mains, Mycologia **42**: 582. 1950. On stromata preceding perithecial formation or on synnemata of similar structure; phialides arising laterally from the outer longitudinal hyphae, variable, subcylindric with one or more constrictions, 10–30 × 4–5 μ, attenuated into acute or acuminate apices 8–14 μ long; conidia ellipsoid to broadly fusoid, 4–8 × 2–2.5 μ, single, hyaline.

On scale insects, Homoptera, Coccidae. Specimens studied: 57 from Connecticut (FH), Delaware (NY), District of Columbia (BPI, CUP, FH), Indiana (BPI), Maine (FH), Michigan (FH, MICH), New Hampshire (BPI, CUP), New Jersey (NY), New York (CUP, FH, NY), North Carolina (FH), Tennessee (FH), Vermont, (BPI), New Brunswick (FH), Ontario (BPI, CUP, FH, NY), Quebec (BPI, CUP, MICH, NY).

This species occurs on scale-insects of the genus *Lecanium*. The insect is usually covered by the gray mycelium. The perithecia are closely crowded in a soft layer which shrinks so that the upper portions protrude, giving a pronounced verrucose appearance to the heads (FIG. 15). The clavate, short, wide asci (FIG. 16) and the clavate ascospores which do not break into part spores are typical of the genus *Ophiocordyceps* as recognized by Petch.

11. CORDYCEPS MILITARIS (Fr.) Link, Handbuch **3**: 347. 1833. (FIGS. 17–19).

Sphaeria militaris Fr. Syst. Myc. **2**: 322. 1823.

Cordylia militaris Fr. ex Ficinus & Schubert, Fl. Dresden 2 ed. **2**: 331. 1823.

Torrubia militaris Tul. Sel. Fung. Carp. **3**: 6. 1865.

Stromata clavate rarely furcate, compressed or terete, frequently with a longitudinal furrow, 0.8–7 cm long, 2–6 mm wide above, orange buff to mikado orange, rough above from the apices of the perithecia, with a stipe 1.5–3 mm thick, with stipe and central core of the upper ascogenous portion consisting of longitudinal parallel to somewhat interwoven hyaline hyphae; perithecia ovoid, 500–720 × 300–480 μ, with a wall 20 μ thick, pseudoparenchymatous in section below, consisting of more or less parallel outwardly diverging hyphae around the ostiole, embedded at right angles to the surface except for apices, in a layer over the upper part of the stroma consisting of loosely outwardly interwoven hyphae without a differentiated cortex; asci narrowly cylindric, 300–510 × 3.5–5 μ, with a 3.5–5 μ thick cap; ascospores filiform, multiseptate, finally breaking into 1-celled fragments, 2–4.5 × 1–1.5 μ.

Usually on pupae, less commonly on larvae of Lepidoptera. Specimens studied: 181 from Alabama (BPI), Connecticut (FH, NY), Florida (MICH), Illinois (MICH), Iowa (BPI, NY), Maine (BPI, FH, NY, MICH), Maryland (BPI), Massachusetts (BPI, CUP, FH, NY), Michigan (MICH), Missouri (BPI, NY), New Hampshire (FH, NY), New Jersey (BPI, CUP, NY), New York (BPI, CUP, FH, NY), North Carolina (BPI, CUP, FH, NY), Ohio (BPI), Oregon (MICH), Pennsylvania (BPI, NY), Rhode Island (FH), Tennessee (BPI, FH, MICH), Vermont (BPI, FH, NY), Virginia (BPI, MICH, NY), Washington (MICH), West Virginia (BPI, CUP, NY), Wisconsin (FH), Nova Scotia (NY), Ontario (MICH, NY), Quebec (BPI, CUP, MICH, NY), Dominican Republic (NY), Puerto Rico (NY).

There are several specimens at Cornell and one in the Farlow Herbarium which Petch determined as *C. miryensis* Henn. Petch (**1933**) at

one time decided that *C. miryensis* was *C. militaris*. He later apparently decided that it was distinct. The North American specimens appear to be variants of *C. militaris*.

C. militaris is the most common of the species on insects and is widely distributed not only in North America but also in South America, Europe and Asia. It is variable in form and especially in size, which is apparently correlated with the food available for development, influenced by the size of host and number of stromata.

The perithecia of *C. militaris* are embedded at right angles to the surface, except for the apices, in a soft loose layer consisting of loosely interwoven hyphae (FIG. 18). There is no well differentiated cortex and the loose tissue shrinks on drying so that the perithecia often appear to be only half embedded or sometimes superficial.

Isaria farinosa has commonly been reported as the conidial stage. Petch (**1936**) obtained a species of *Cephalosporium* in cultures from ascospores of *C. militaris* and has concluded that *Isaria farinosa* is not connected. Kobayasi (**1941**) has reached similar conclusions.

12. CORDYCEPS WASHINGTONENSIS Mains, Mycologia **39**: 535. 1947. (FIG. 20).

Stromata fusoid-cylindric to narrowly clavate, 15–30 mm long, 2–6 mm wide, sulphur-yellow when young, pinard yellow with age, sordid white when dried, rough above from the apices of the perithecia, the stipes whitish, 2–4 mm thick, with the stipe and central core of the upper ascogenous portion consisting of compact parallel longitudinal hyphae; perithecia ovoid, 450–644 × 252–386 μ, with the wall well differentiated, 15–20 μ thick, completely embedded at right angles to the surface in a layer covering the stroma consisting of loosely to closely interwoven hyphae without a differentiated cortex; asci clavate, 300–418 × 3–3.5 μ, with a 2 μ thick cap; ascospores subclavate, 80–110 × 1–1.5 μ, multiseptate, part-spores not seen.

On pupae and larvae of Lepidoptera. Washington, *E. B. Mains 6185*, TYPE, *6204; E. B. Mains and A. H. Smith 6232* (all MICH).

The soft, loose tissue between the perithecia when dried shrinks and conforms to the upper portion of the perithecia, causing them to appear partly embedded.

C. washingtonensis is closely related to *C. militaris* from which it differs in its lighter color, clavate asci and ascospores.

13. CORDYCEPS ELONGATA Petch, Brit. Myc. Soc. Trans. **21**: 47. 1937. (FIG. 21).

Stromata slender, cylindric, 3.5–11 cm long, with apices acute, rarely sterile, with upper ascogenous portion 0.8–2 mm thick, yellowish or

light yellow-brown, punctate from apices of perithecia, with stipes 0.5–1.5 mm thick, light brown or brownish gray, with central core of stipe and ascogenous portion consisting of hyaline compact longitudinal somewhat interwoven hyphae, with outer hyphae of the stipe longitudinal, parallel and brown; perithecia narrowly ovoid, 350–480 × 180–300 μ, light brown, with wall well differentiated, 25 μ thick, entirely embedded at right angles to the surface in a layer covering the stroma consisting of loosely interwoven hyphae below and more closely interwoven above but without a well differentiated cortex; asci cylindric, 200–300 × 8 μ, with a 4 μ thick cap; ascospores filiform, 150–175 × 2 μ, multiseptate, the cells 12–20 μ long, part-spores not seen.

On larvae of Lepidoptera, *Acronicta* (*Apatela*) *americana*. Maine, *R. Thaxter*, FH 6137, TYPE. North Carolina, *R. Thaxter*, FH 6135, FH 6277. Tennessee, *R. Thaxter*, FH 3906, FH 6134.

This species is closely related to *Cordyceps militaris*. It differs in the long slender cylindric stromata (FIG. 21) with light yellow ascogenous portion and brownish stipe and in somewhat broader asci and ascospores with longer cells for the ascospores.

Petch (l.c.) has suggested that the conidial stage of this species is *Hirsutella gigantea* Petch. The specimen previously reported from British Honduras (Mains, **1940b**) as *C. elongata* consists of only one stroma having much smaller cells for the ascospores. The determination is doubtful.

14. CORDYCEPS OLIVASCENS Mains, Mycologia **39**: 537. 1947.

Stroma narrowly clavate, 4 cm long, the upper ascogenous portion 2.5 mm thick, olive-buff to deep olive-buff when fresh, citrine-drab dried, with a stipe 1–2 mm thick, dark olive, with the stipe and central core of the upper ascogenous portion of compact longitudinal somewhat interwoven hyphae; perithecia conoid or narrowly ovoid, 900–1200 × 240–374 μ, with a thin 10–15 μ wall, completely embedded at right angles to the surface in a layer covering the upper portion of the stroma consisting of loosely interwoven greenish hyphae below, more closely interwoven and greenish brown above, without a well differentiated cortex; asci cylindric, 480–600 × 4–6 μ, with a 2–2.5 μ cap; ascospores filiform, multiseptate, breaking into 1-celled fragments 3–4 × 1 μ.

On fragments of an insect. Alabama, *R. P. Burke*, TYPE (MICH).

This species is known only from the type. Only fragments of the host were left and the identity of the insect is unknown. A comparison of this species with other green species of *Cordyceps* has been made elsewhere (Mains, **1947**).

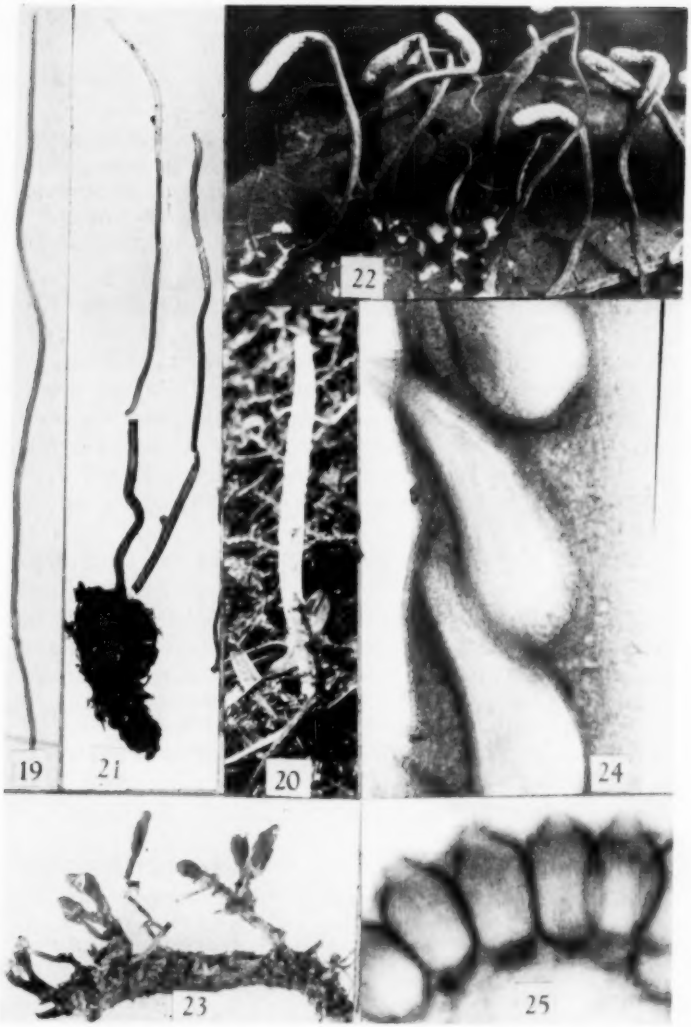


FIG. 19, *C. militaris*, ascus, × 300. FIG. 20, *C. washingtonensis*, stroma, × 2. FIG. 21, *C. elongata*, stroma, × 1. FIG. 22, *C. polyarthra*, stromata, × 2.5. FIGS. 23–24, *C. martialis*; 23, stromata, × 1; 24, oblique perithecia, × 75. FIG. 25, *C. macularis*, type, perithecia, × 75.

15. CORDYCEPS CALOCEROIDES Berk. & Curtis, Jour. Linn. Soc. **10**: 375. 1869.

Ophiocordyceps caloceroides Petch, Brit. Myc. Soc. Trans. **18**: 63. 1933.

Stromata simple or furcate, up to 11.5 cm long, with branches 6–8 cm long, reddish brown, the stipes 0.5–1 mm thick, the upper perithecial portion slightly thicker, 1–2 mm thick; perithecia ovoid to ellipsoid, 200–250 × 85–150 μ, very crowded, the walls poorly differentiated, with closely interwoven hyphae between the apices; asci cylindric, 90–175 × 3–4 μ, with a 2 μ thick cap; ascospores not seen.

On an unidentified host, probably a spider. Cuba, *Charles Wright 749*, TYPE (K, FH).

This species has been discussed elsewhere (Mains, **1954**). A fragment of the type in the Kew Herbarium has been seen and there is a specimen in the Curtis Collection of the Farlow Herbarium which is probably part of the same collection. No host is given. *Cordyceps wittii* on a spider from Ecuador is very similar (Petch, **1933**). It seems probably that the host of *C. caloceroides* is the same.

16. CORDYCEPS GRENADENSIS Mains, Bull. Torrey Bot. Club **81**: 499. 1954.

Stromata 10–12 mm long, red, subcapitate, the heads ovoid to cylindric 1.5–2 × 1 mm, the stipes slender, 0.5 mm thick; perithecia ovoid, 336–360 × 156–216 μ, red, partly embedded at right angles to the surface of the head in a soft, yellowish red tissue consisting of loosely interwoven hyphae; asci narrowly clavate, 180–252 × 4 μ, with a 2–3 μ thick cap; ascospores filiform 50–70 × 1 μ, multiseptate, the cells 4–5 μ long, not breaking into part-spores.

On a ground spider, Arachnida. Grenada, B. W. I., *R. Thaxter*, FH 6122, TYPE.

This species is known only from the type specimen. It differs from *C. caloceroides* in having much smaller capitate stromata, larger perithecia and asci.

17. CORDYCEPS POLYARTHRA Möller, Phyco. u. Asco. 213. 1901. (FIG. 22).

Cordyceps concurrens Lloyd, Myc. Writ. **7**: 1180. 1922.

Stromata many, cespitose, narrowly clavate, 15–20 mm long (up to 5.5 cm Möller), with the upper ascogenous portion cylindric to narrowly clavate, 0.5–1.5 mm thick, light yellow except for the reddish brown perithecia, with the stipes 0.3–0.4 mm thick and reddish brown

to light yellow, with stipes and central core of perithecial portion consisting of compact longitudinal somewhat interwoven brownish hyphae; perithecia ovoid, 250–450 × 125–250 μ, brown, with a definite wall 25 μ thick, embedded at right angles to the surface in a soft layer consisting of moderately to closely interwoven hyaline to yellowish hyphae without a definite cortex, with apices of perithecia finally projecting due to shrinkage of tissue; asci cylindric, 150–260 × 3–4 μ, with a 1.5–2 μ thick cap; ascospores filiform (part spores 4–6 × 0.75–1 μ according to Petch, **1929**); synnemata similar to the stromata, clavate, up to 1 cm long, white pulverulent; conidia ellipsoid, 2–2.5 × 1–1.5 μ, hyaline.

On larvae of Lepidoptera. Costa Rica, *Dodge and Goerger 9297* (BPI). Panama, on *Brassolis isthmia, Bro. G. Regis,* FH 6129 (as *C. michaelisii*).

These specimens differ principally from the description of *C. polyarthra* as given by Möller in having shorter stromata. A number of species have been described which are very similar except for size. Petch (**1933**) has concluded that *C. subpolyarthra* Henn., *C. caespitosa-filiformis* Henn., *C. concurrens* Lloyd and *C. fasciculata* Pat. are *C. polyarthra.* The type of *C. fasciculata* in the Farlow Herbarium has a red, irregularly dichotomously branched stroma and is not *C. polyarthra.* As discussed elsewhere (Mains, **1958**) the type of *C. concurrens* except for shorter stromata and somewhat smaller conidia agrees with the description given by Möller. Petch apparently saw the types of *C. subpolyarthra* and *C. caespitosa-filiformis* but does not give much additional information. Hennings (**1902**) described another species, *C. michaelisii,* which also appears to be *C. polyarthra.* Vital (**1956**) has also described a species, *C. exasperata,* which he distinguished from *C. polyarthra* principally by shorter stromata.

Petch (**1933**) has concluded that the conidial stage of *C. polyarthra* is *Isaria dussii* Pat. (*I. palmatifida* Henn., *Gibellula eximia* Höhnel).

18. CORDYCEPS SOBOLIFERA (Berk.) Berk. & Br. Jour. Linn. Soc. **14**: 110. 1875. (FIGS. 26, 27).

Sphaeria sobolifera Berk. Hook. Lond. Jour. Bot. **2**: 207. 1843.
Torrubia sobolifera Tul. Sel. Fung. Carp. **3**: 10. 1865.

Stromata clavate, simple or with conidial branches below on stipe, 2.5–8 cm long, 2–6 mm thick above, with the stipe 0.5–3 mm thick, light buff, reddish brown or purplish brown, with central core of the stipe and upper ascogenous portion consisting of compact longitudinal somewhat interwoven hyaline or brownish hyphae, with a thin layer of closely to loosely interwoven brown hyphae covering the stipe; perithecia conoid or narrowly ovoid, 500–720 × 170–250 μ, with a well differentiated

brown wall 20–25 μ thick, completely embedded at right angles to the surface in a layer covering the upper part of the stroma consisting of loosely interwoven hyaline hyphae below, becoming closely interwoven and brown below the surface but without a well differentiated cortex; asci cylindric, 300–400 × 5–7 μ, with a 4 μ thick cap; ascospores filiform, multiseptate breaking into 1-celled fragments, 6–12 × 1–1.5 μ.

Conidial stage: *Isaria cicadae* Miquel (see Petch **1933**, p. 65). On branches of the stipes of perithecial stromata (FIG. 26) or branches from the apices of synnemata of similar structure (FIG. 27); conidiophores forming a tangled mat; phialides arising directly as lateral cells or terminating short branches, forming small heads, obovoid with acute apices, 4–5 × 2 μ; conidia oblong, 6–10 × 2–3 μ hyaline.

On Homoptera, Cicadidae. Florida, on *Diceroprocta olympusa, T. H. Hubbell* (MICH). Bahamas, *L. J. K. Brice*, LH 35613, LH 35614 (BPI). Cuba, *S. C. Bruner* (BPI). Mexico, *R. Thaxter*, FH 6191; *W. G. Johnson* (BPI); Jalisco, *Albert E. Maas* (BPI).

This species has also been reported from Dominica, Martinique, Guadaloupe, St. Thomas and Jamaica. It is most frequently collected in the conidial state, which has been described under a number of names (Petch, **1933**). Kobayasi (**1941**) has stated that *C. sobolifera* in Japan has a pycnidial stage and has questioned a connection with *Isaria cicadae*. However, *C. sobolifera* was described from the West Indies and, as Petch (**1942**) has pointed out, West Indian and Mexican collections leave no room for doubt that the *Isaria* is the conidial stage. The specimen reported from Ceylon on a lamellicorn insect by Berkeley and Broome in transferring *Sphaeria sobolifera* from *Sphaeria* to *Cordyceps* was *Cordyceps barnesii*, according to Petch (**1934**).

19. CORDYCEPS MARTIALIS Speg. Bol. Acad. Nac. Cordova **11**: 305. 1889. (FIGS. 23, 24).

Cordyceps hunti Giard, Bul. Soc. Entom. France **64**: CLXXI. 1895.

Cordyceps submilitaris Henn. Hedwigia **36**: 222. 1897.

Cordyceps klenei Pat. Bul. Soc. Myc. France **24**: 11. 1908.

Stromata usually attached to the host by orange or red rhizomorphs, cylindric to clavate, usually with acute apices, 1–3 cm long, the upper ascogenous portion 2–4 mm thick, the stipe 1–2 mm thick, rough above from protruding apices of the perithecia, brownish, red, orange-yellow, orange or cinnabar, with the stipe and central core of the ascogenous portion consisting of compact longitudinal parallel or somewhat interwoven narrow hyaline hyphae; perithecia narrowly ovoid or conoid, 650–840 × 240–450 μ, embedded except for apices obliquely to the surface in a layer consisting of loosely to closely interwoven hyphae without

a well differentiated cortex; asci narrowly cylindric, 300–510 × 3–4 μ with a 2 μ thick cap; ascospores filiform, multiseptate, 0.5–1 μ thick, tardily breaking into part-spores 6–10 μ long.

On larvae of Coleoptera. British Honduras, *E. B. Mains 3686, 3836* (MICH).

Specimens have also been seen from British Guiana (FH) and Brazil (BPI, FH, Herb. Spegazzini = TYPE). Petch (**1934**) has suggested that *Cordyceps pittieri* Bomm. & Rouss., which was described from Costa Rica, is probably *C. martialis*. Kobayasi (**1941**) includes it as a synonym of *C. melolonthae*.

This species has some resemblance to *C. militaris*, especially in color, and occurs in herbaria misidentified as such. It, however, infects coleopterous larvae, which are covered by an orange or red mycelium, and the stromata are usually attached in the host by orange or red rhizomorphs (FIG. 23). It also differs in that the perithecia are embedded obliquely to the surface (FIG. 24). Spegazzini did not note this oblique arrangement but the type, which has been available for study through the kindness of J. C. Lindquist, shows the oblique arrangement. Likewise, the type of *C. klenei* in the Patouillard Collection of the Farlow Herbarium has oblique perithecia, although Patouillard illustrates them as embedded at right angles to the surface. This species also occurs in herbaria and in the literature as *C. lunti*, a name which apparently was first used instead of *C. hunti* by Ferry (**1899**).

20. CORDYCEPS MACULARIS Mains, Papers Mich. Acad. Sci. **25**: 82. 1940. (FIG. 25).

Ophiocordyceps macularis Mains, Proc. Am. Phil. Soc. **74**: 269. 1934.

Stromata slender, cylindric, acuminate above, 20–35 mm long, 1 mm thick, light ochraceous salmon or vinaceous fawn, consisting of compact parallel longitudinal hyaline to brownish hyphae with an outer thin (20 μ) layer of outwardly interwoven brownish hyphae; perithecia ovoid, 290–325 × 190–225 μ, few to many, very closely crowded in irregular lateral cushions, with wall 15–20 μ thick; embedded in a tissue consisting of moderately interwoven hyphae below, becoming more closely interwoven above; asci clavate or subfusoid, 130–180 × 6–8 μ, with 2–3 μ thick caps; ascospores subfusoid, 60–90 × 2–3 μ, multiseptate, with cells 6–14 μ long, part-spores not seen.

On larvae of Coleoptera. Michigan, *E. B. Mains and A. H. Smith 33–453*, TYPE (MICH). New York, *A. H. Smith 844* (MICH).

The perithecia of this species are produced in lateral cushions which

vary in number and size. The perithecia are embedded and occupy most of the cushion with loosely interwoven hyphae between the bases and with closely interwoven hyphae covering and conforming to the upper portions of the perithecia, giving an irregular surface to the cushion. Oblong cells with acuminate apices, probably phialides, occur scattered in the thin outer layer of the stromata. Conidia were not found attached but free subgloboid cells $2.5 \times 2\,\mu$, probably conidia, occur.

21. CORDYCEPS MELOLONTHAE (Tul.) Sacc. Michelia **1**: 320. 1879.
Torrubia melolonthae Tul. Sel. Fung. Carp. **3**: 12. 1865.

Stromata clavate, sometimes somewhat furcate, 3–13 cm long, with upper ascogenous portion 5–15 mm wide, sulphur-yellow to mikado-orange above when fresh, yellowish brown when dried, with stipes 4–6 mm thick, light buff when fresh, yellowish brown dried, with stipe and central core of the ascogenous portion of compact longitudinally interwoven hyphae; perithecia ovoid, $360–480 \times 170–264\,\mu$, embedded except for the apices at right angles to the surface in a layer consisting of closely interwoven hyaline to brown hyphae without a differentiated cortex, with walls $20\,\mu$ thick, with ostioles lined with periphyses; asci cylindric, $210–300 \times 6–8\,\mu$, with $2–3\,\mu$ thick caps; ascospores filiform, multiseptate breaking into 1-celled fragments $4–8 \times 1–1.5\,\mu$.

On larvae of Coleoptera, Scarabaeidae.

VAR. MELOLONTHAE (FIG. 28).

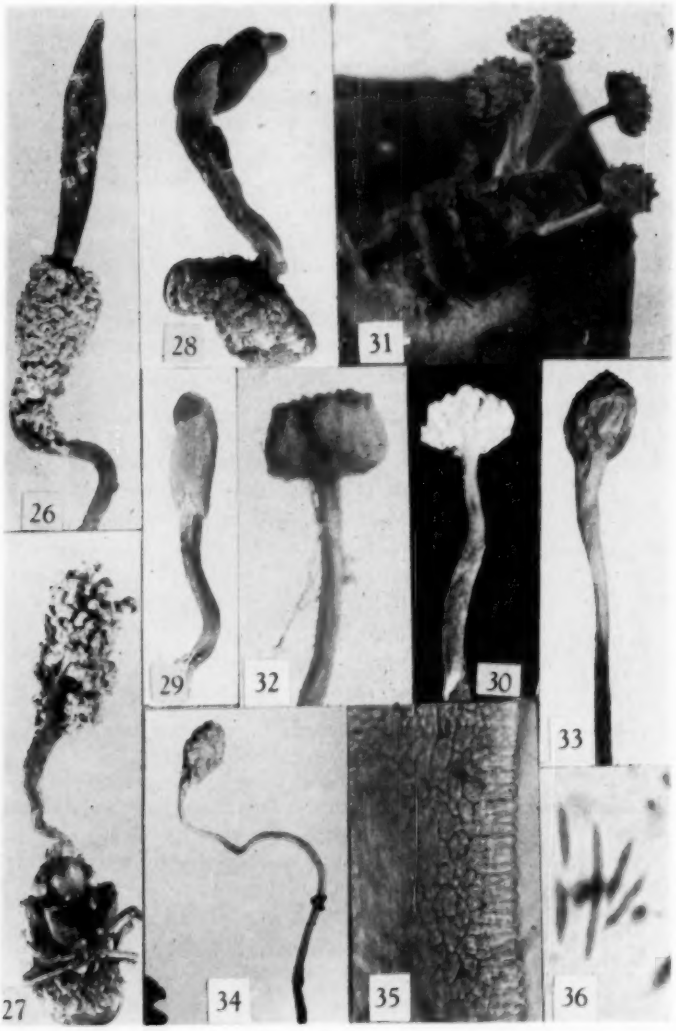
Perithecial layer developing in patches, sometimes coalescing and surrounding the stroma but with apices of stromata sterile.

"Carolina," *R. Thaxter,* FH 6184. Kentucky, *C. W. Hibbard* (BPI). Michigan, *E. B. Mains; A. H. Smith 1718, 18498; L. E. Wehmeyer; H. D. Thiers 3373* (MICH). New York, *G. F. Atkinson; P. G. Chapman; K. D. Scott; Mrs. Harry Hale* (CUP); *W. L. Bosworth* (BPI). Ohio, *A. P. Morgan* (NY). Tennessee, *A. H. Smith 9893, 10245* (MICH); *C. A. Wright* (BPI). Virginia, *W. A. Murrill* (NY). Wisconsin, *Trelease,* FH 6164.

VAR. **rickii** (Lloyd) comb. nov. (FIG. 29).
Cordyceps rickii Lloyd, Myc. Writ. **6**: 914. 1920.

Perithecial layer completely covering the upper part of the stroma.

Nicaragua, *P. W. Oman* (BPI). Specimens of this variety have also been seen from Brazil (BPI), British Guiana (FH), Trinidad



FIGS. 26–27, *C. sobolifera;* 26, stroma with conidial branches, × 1; 27, synnema, × 1. FIG. 28, *C. melolonthae,* stroma, × 1. FIG. 29, *C. melolonthae* var. *rickii,* type, stroma, × 1. FIG. 30, *C. salebrosa,* type, stroma, × 10. FIG. 31, *C. dipterigena,* stroma, × 5. FIG. 32, *C. lloydii,* stroma, × 10. FIG. 33, *C. curculionum,* stroma, × 6. FIGS. 34–36, *C. sphecocephala;* 34, stroma, × 6; 35, cortex, × 500; 36, part-spores, × 1000.

(FH). *Cordyceps cusu* Pat. from Ecuador, based on a sterile specimen, is probably this variety (Mains, **1940c**).

In the United States the variety *melolonthae* infects the large larvae of the "June bug" or "May beetle" of the genus *Phyllophaga*. The perithecial layer develops in patches which sometimes coalesce and surround the stroma but the apex is always sterile (FIG. 28). The variety *rickii* differs mostly in that the perithecial layer always completely covers the upper part of the stroma (FIG. 29). This variety appears to be limited to tropical North and South America.

There is considerable confusion and uncertainty concerning the nomenclature of this species (see Petch, **1934**). The variety *melolonthae* is frequently found in herbaria and has been reported in the literature as *Cordyceps herculea* (Schw.) Sacc. Lloyd (**1913**) has shown that *Sphaeria herculea* Schw. is a Gasteromycete, *Cauloglossum transversarium*. Lloyd reported it as *C. insignis*, which is a different species. It has generally been named *C. melolonthae* in recent years. There is some question concerning the validity of this name because Tulasne based it on illustrations by Cist (**1824**) of sterile stromata on larvae of the "May-bug." They are not typical and might equally as well be sterile stromata of *C. ravenelii*. Other names which have been considered synonyms are *C. volkiana* Möller (Petch **1934**) and *C. pittieri* Bomm. & Rouss. (Kobayasi, **1941**). Both are doubtful.

II. SUBGENUS CORDYCEPS. SECTION 3. CREMASTOCARPON

22. CORDYCEPS ARMENIACA Berk. & Curt. Jour. Linn. Soc. **1**: 158. 1857.

Stroma capitate, 5 mm long, the head hemispherical, reniform in section, 1.2 mm wide, 0.6 mm thick, reddish brown, punctate from the ostioles, the stipe slender, 0.2 mm thick, brownish yellow, consisting of compact longitudinal parallel light brown hyphae; perithecia narrowly ovoid, 450–650 × 220–250 μ, crowded, the wall 15–20 μ thick, with periphyses lining the ostiole, completely embedded with ostioles opening on the upper surface of the head in a tissue of closely interwoven brown hyphae with an ectal palisade-like layer 20 μ thick of hyaline hyphae; asci cylindric, 150–175 × 3–4 μ, with a 3 μ thick cap; ascospores filiform, immature.

Host not identified. South Carolina, Society Hill, Curtis Coll. 3774, part of TYPE (FH).

The specimen in the Curtis Collection of the Farlow Herbarium apparently is part of the collection which Curtis sent to Berkeley, since it bears the number 3774 cited by Berkeley. The host is uncertain. Berkeley states "apparently on the excrement of birds but probably on

larvae contained in it." The species is known only from the one collection.

23. CORDYCEPS SALEBROSA Mains, Mycologia **39**: 541. 1947. (FIG. 30).

Stromata 3.5–4 cm long, capitate, the heads flattened oblate-globoid, 1–1.5 mm, light cream colored when dry, red when fresh, the upper surface very irregular, the stipes 0.2–0.3 mm thick, brownish black below, concolorous with the head above, within consisting of compact longitudinal somewhat interwoven hyphae diverging above and becoming very loosely interwoven in the base of the head, having a thin cortex of pseudoparenchyma; perithecia narrowly ovoid or conoid, 840–1200 × 240–300 μ, vertical with ostioles on the upper surface of the head, completely embedded in a tissue consisting of very loosely interwoven hyphae with a very thin, 15–20 μ compact ectal layer of oblong or globoid cells; asci cylindric, 600–660 × 6 μ, with a 5 μ thick cap; ascospores filiform, multiseptate, breaking into 1-celled fragments, 6–10 × 1–1.5 μ.

On adult beetle, Coleoptera, Elateridae, Panama Canal Zone, *L. Hare*, TYPE (MICH).

This species is known only from the type. On the one hand it is similar to *C. dipterigena* on flies, differing in having a bicolored stroma, and on the other it is like *C. curculionum* on beetles, differing in having a flattened head.

24. CORDYCEPS DIPTERIGENA Berk. & Br. Jour. Linn. Soc. **14**: 111. 1875. (FIG. 31).

Cordyceps muscicola Möller, Phyco. u. Asco. 221. 1901.

Cordyceps oumensis Höhnel, Sitz. Akad. Wiss. Wien **118**: 309. 1909.

Cordyceps opposita Syd. Engler Bot. Jahrb. **57**: 325. 1922.

Stromata one to several from the host, 2.5–8 mm long, capitate, the heads hemispherical or oblate globoid, 1–2 mm wide, 0.5–1 mm thick, orange-cinnamon or cinnamon-brown, rough on the upper surface from apices of the perithecia, the stipes cylindric, 0.2–0.5 mm thick, orange-cinnamon to light yellow, consisting of compact longitudinal somewhat interwoven hyphae continuing into the base of the head, becoming very loosely interwoven; perithecia narrowly ovoid or conoid, 700–900 × 240–400 μ, vertical with the ostioles opening on the upper surface of the head, the wall brownish, thin, 15–25 μ, completely embedded in a tissue consisting of very loosely interwoven hyaline hyphae with a thin, 25–75 μ, cortex of brown pseudoparenchyma and an ectal layer of hyaline or brownish oblong cells; asci cylindric 480–600 × 4–6 μ, with a 4 μ

cap; ascospores filiform, multiseptate, finally breaking into cylindric or fusoid fragments, 6–12 × 1–1.5 μ.

Conidial stage: *Hymenostilbe dipterigena* Petch, Brit. Myc. Soc. Trans. **16**: 212. 1932 (also Mains, **1950**). Synnemata frequently accompanying the stromata, subcylindric, 4–12 mm long, 0.2–0.5 mm thick, brown; phialides forming a dense palisade layer, cylindric to clavate, 14–18 × 3–4 μ, bearing cylindric to slightly capitate projections over the apices; conidia obovoid, 4–9 × 2–4 μ, hyaline, borne singly.

On flies, Diptera. Alabama, *H. K. Plank* (BPI). Mississippi, *L. K. Miles* (BPI). North Carolina, *R. Thaxter*, FH 4052, 5077, 5086, 6233C, Reliq. Farl. 612. Tennessee, *R. Thaxter*, FH 6192. Cuba, *G. C. Bruner* (BPI). Costa Rica, *J. R. Johnston*, FH 4034. Nicaragua, *Kevorkian and Cruz* (BPI). Puerto Rico, *J. A. Stevenson*, LH 41283 (BPI). Specimens also seen from Brazil, British Guiana and Trinidad.

Massee (**1895**) gives a description taken from the type specimen collected by Thwaites in Ceylon and Lloyd (**1921**) has published photographs of the type. This species has been described under a number of names. In addition to the synonyms given here Petch (**1932**) includes *C. surinamensis* Henn. From Hennings's (**1902**) description this is doubtful. *Cordyceps thwaitesii* Lloyd and *C. musae* Henn. appear to be immature specimens. Petch (**1921, 1932**) has concluded that *C. coccigena* (Tul.) Sacc. is the same as *C. dipterigena*. If so, the name of the species should be *C. coccigena*. Tulasne (**1865**) described *Torrubia coccigena* from a collection from New Guinea. He gives the host as a scale insect, *Coccus*. From his figure this is doubtful and it is possible that it is a fly. Lloyd (**1916b**) states that a specimen of this fungus does not occur in the Tulasne Herbarium. Without positive proof it would be unfortunate to adopt the name for this species.

The hosts of this species are usually attached to the substratum by mycelium which spreads out, forming thin yellowish or brownish crusts several millimeters wide.

25. CORDYCEPS LLOYDII Fawcett, Ann. Mag. Nat. Hist. XVIII. **5**: 317. 1886. (FIG. 32).

Stromata 3–5 mm long, capitate, the heads hemispherical, flattened globoid or flattened turbinate, 1–2 mm wide, 0.5–1 mm thick, light yellow to brownish yellow, the stipes slender, 0.2–0.3 mm thick, consisting of compact longitudinal somewhat interwoven brownish hyphae diverging above and becoming very loosely interwoven in the base of the head, covered with scattered to crowded oblong hyaline cells; peri-

thecia narrowly ovoid to conoid, 600–950 × 210–300 μ, the brownish wall 25–35 μ thick, vertical with ostioles opening on the upper surface of the head, completely embedded in a tissue consisting of very loosely interwoven hyaline hyphae with a thin, 40 μ, cortex of brownish pseudoparenchyma with an ectal layer of oblong hyaline cells; asci cylindric, 500–750 × 4.5–6 μ, with a 4–6 μ cap; ascospores filiform, multiseptate, breaking into 1-celled fusoid fragments 7–12 × 1.5–2 μ.

On ants, Hymenoptera, Formicidae, *Camponotus* spp. Panama, *C. F. W. Muesebeck* (BPI). Specimens have also been seen from Trinidad (FH).

Petch (**1932**) has reported that the conidial stage of this species is *Hymenostilbe formicarum* Petch, based on a collection from British Guiana having one specimen bearing perithecial stromata and another with conidial synnemata. The phialides are described as cylindric, 24 × 4 μ, verrucose above with one or two broad truncate sterigmata and the conidia as narrow-clavate or subcylindric, 6–11 × 1–1.2 μ.

Petch (**1931**) states that the type of *Cordyceps sherringii* Massee on an ant from Grenada, West Indies is an immature *C. lloydii*. Petch (**1932**) also states that an examination of the type specimen of *C. subdiscoidea* Henn. shows that it is *C. lloydii*. Hennings (**1902**) described the asci of *C. subdiscoidea* as 100–130 × 3 μ. Unfortunately, Petch does not give information concerning the type. *C. lloydii* is very similar to *C. dipterigena* on flies.

26. CORDYCEPS CURCULIONUM (Tul.) Sacc. Michelia **1**: 320. 1879.
Torrubia curculionum Tul. Sel. Fung. Carp. **3**: 20. 1865.
Cordyceps bicephala subsp. *curculionum* Moureau, Mem. Inst. Roy. Col. Belge **7** (fasc. 5): 50. 1949.

Stromata 4–4.5 cm long, capitate, the head ovoid, 1.5–2 × 1–1.5 mm, strawberry- to cinnamon-pink when fresh, cream to brownish yellow when dried, the stipe slender, 0.5–1 mm thick, brownish black to black below, concolorous with the head above, consisting of compact longitudinally somewhat interwoven, hyaline to brownish hyphae, diverging and becoming loosely interwoven in the head; perithecia conoid, often somewhat curved, 780–1020 × 264–300 μ, with a well differentiated brownish wall, completely embedded obliquely to the surface in a tissue of loosely interwoven hyphae between the perithecia, with a cortex of brownish pseudoparenchyma having an ectal layer 1 cell thick of oblong hyaline cells; asci cylindric, 650–750 × 5–6 μ, with a 3–6 μ thick cap; ascospores filiform, multiseptate, breaking into fusoid, 1-septate segments, 10–12 × 1.5–2 μ.

On adult beetles, Coleoptera, Curculionidae. British Honduras, *E. B. Mains 3689* (MICH). Jamaica, *A. H. Ritchie,* LH 35624, 35625 (BPI). Panama Canal Zone, *B. Lowy.* This species has also been reported from Peru, Ecuador, Brazil and Belgian Congo.

Cordyceps australis (Speg.) Sacc. on ants and *C. nutans* Pat. on Hemiptera are very similar to *C. cucurlionum.* Except for a few minor differences the hosts are the principal distinctions. Moureau (**1949**) considers *C. australis* to be a synonym of *C. bicephala* Berk. and treats the three as subspecies of *C. bicephala.* As discussed elsewhere (Mains **1949**), the identity of *C. bicephala* is uncertain because the host is unknown. It is probably one of the three species and therefore would be earliest name for the composite species, but it is uncertain to which it would belong. It seems best here to treat *C. curculionum* as a species. *C. australis* and *C. nutans* have not been reported from North America. *C. australis* has been reported from Liberia, Belgian Congo, British Guiana and Brazil and probably occurs in tropical North America. *C. nutans* has been reported from Japan, China and the Belgian Congo.

27. CORDYCEPS SPHECOCEPHALA (Berk.) Sacc. Michelia **1**: 321. 1879. (FIGS. 34–36).

Sphaeria sphecocephala Berk. Hook. Lond. Jour. Bot. **2**: 206. 1843.

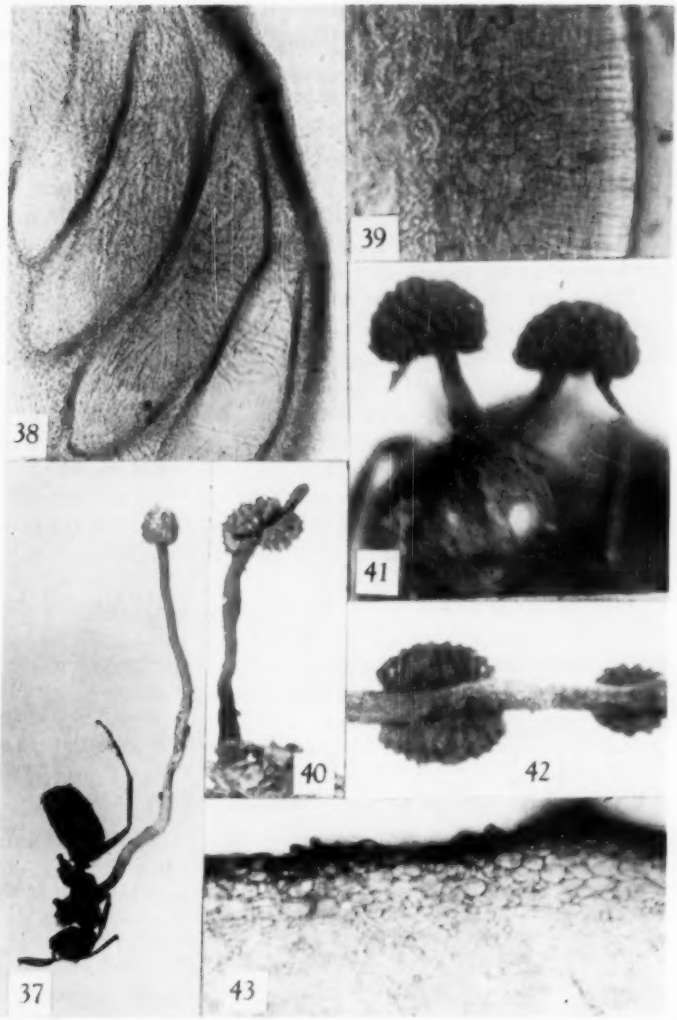
Polistophthora antillarum Lebert, Grebold, Zeitschr. Wiss. Zool. **9**: 452. 1858.

Torrubia sphecocephala Tul. Sel. Fung. Carp. **3**: 18. 1865.

Cordyceps sphecophila Berk. & Curt. Jour. Linn. Soc. **10**: 376. 1869.

Stromata 2–10 cm long, capitate, the heads ovoid, obovoid or subcylindric, 2–8 × 1.5–3 mm, light cream to brownish yellow, longitudinally irregularly rugose when dry, the stipes 0.3–1 mm thick, concolorous with the heads, the stipe and central core of the head consisting of compact longitudinal parallel to somewhat interwoven brownish hyphae; perithecia conoid, 900–1200 × 210–300 μ, frequently with the neck curved, entirely embedded obliquely to the surface in a tissue consisting of very loosely interwoven hyphae below with a cortex having a thin layer of brown pseudoparenchyma and an ectal layer 1 cell thick of oblong hyaline cells; asci cylindric, 450–660 × 5–7 μ with a 6 μ thick cap; ascospores filiform, multiseptate, breaking into 1-celled fusoid segments 8–12 × 1.5–2 μ.

On wasps, Hymenoptera, Vespidae, *Polistes, Tachytes* and *Vespa* spp. Florida, *R. Singer F 949, F 1518, F 1603* (FH); *J. B. McFarlin 38* (BPI). Georgia, *Charles H. Driver 625B.* Tennessee, *Stevenson*



FIGS. 37–39, *C. myrmecophila;* 37, stroma, × 3; 38, oblique perithecia, × 75; 39, cortex, × 400. FIG. 40, *C. variabilis,* stroma, × 3. FIGS. 41–43, *C. unilateralis;* 41, stromata, × 10; 42, portion of stroma with lateral perithecial cushions, × 10; 43, cortex, × 400.

& Davidson (BPI); *D. H. Linder* (FH); *A. H. Smith 7399, 7478, 9664, 9938, 10176, 1035* (MICH). Cuba, *R. Thaxter,* FH 4051, FH 4243, FH 6193, Fungi Cub. Wrightiani 751 (FH). Jamaica, *A. H. Ritchie,* LH 35625 (BPI). Puerto Rico, *R. A. Toro* (FH); *A. N. Wolcott* (BPI). It also has been reported from Brazil and China.

In *C. sphecocephala* the longitudinal hyphae of the stipe continued to form a central core of the head. Moureau states that in some collections this central core may continue to form a short sterile apex. At the base of the head the outer hyphae of the stipe split off from the central core and form a thin layer of parallel longitudinal hyphae part way up the head below a cortex consisting of a thin layer of pseudoparenchyma and an ectal layer of oblong cells (FIG. 35). The perithecia, which are oblique to the surface, develop in a tissue of very loosely interwoven hyphae with the necks penetrating the cortex.

This species has frequently been given the name *C. sphecophila* apparently due to an error in publication by Berkeley and Curtis, who cited Tulasne but changed the name. Petch (**1933**) has concluded that *C. gentilis* (Ces.) Sacc., *C. lachnopoda* Penz. & Sacc., *C. oxycephala* Penz. & Sacc., *C. puiggari* Speg. and *C. thrysoides* Möller are *C. sphecocephala.* As discussed elsewhere (Mains, **1948**) *C. puiggari* is not this species.

Cordyceps tricentrus Yasuda on Hemiptera in Japan and *C. myrmecophila* on ants (see following) are very similar to *C. sphecocephala.* The three are closely related to *C. curculionum, C. nutans,* and *C. australis,* which differ principally in their bicolored stromata.

28. CORDYCEPS MYRMECOPHILA Ces. Bot. Zeit. **4**: 877. 1846. (FIGS. 37–39).

Torrubia myrmecophila Tul. Sel. Fung. Carp. **3**: 18. 1865.

Stromata 0.8–4 cm long, capitate, the heads ovoid, 1.5–4 × 1.5–2 mm, ochraceous, longitudinally rugose when dry, the stipes 1 mm thick, light yellow, consisting of compact longitudinal somewhat interwoven hyphae within, longitudinal and parallel toward the outside, diverging and becoming loosely interwoven in the head; perithecia narrowly ovoid to conoid, 600–1020 × 190–300 μ, with the wall 20–25 μ thick, completely embedded obliquely to the surface in a tissue of loosely interwoven hyphae with a cortex consisting of brownish pseudoparenchyma 50 μ thick and an ectal palisade layer of hyaline septate hyphae 50–60 μ thick; asci cylindric, 480–720 × 4–6 μ, having a 6 μ thick cap; ascospores filiform, multiseptate, breaking into 1-celled fragments 8–10 × 1.5 μ.

On ants, Hymenoptera, Formicidae, *Camponotus* and *Formica* spp. Michigan, *M. Lange,* A.H.S. 25313 (MICH). Oregon, *Gruber &*

Smith 19033 (MICH). Tennessee, *A. C. Cole 10998* (MICH). Washington, *A. H. Smith 13865, 13955, 14006, 14157, 14206, 14274, 14575, 14652* (all MICH). British Columbia, *J. F. Davidson* (MICH).

C. myrmecophila is closely related to *C. sphecocephala*. It differs in having smaller stromata, in the heads lacking a core of longitudinal hyphae and in having a better developed cortex with an ectal palisade layer of septate hyphae.

29. CORDYCEPS VARIABILIS Petch, Brit. Myc. Soc. Trans. **21**: 44. 1937. (FIG. 40).

Cordyceps viperina Mains, Mycologia **29**: 674. Dec. 1937.

Stromata cylindric, acute above, 5–17 mm long, 0.5–1 mm thick, ochraceous to ochraceous orange, furfuraceous, with central core of compact longitudinal parallel to somewhat interwoven hyaline to brownish hyphae, with an outer layer of brown outwardly interwoven hyphae terminating in irregular clumps of brown globoid cells, with perithecia in one to several lateral very variable cushions, punctate to rough from apices of the perithecia; perithecia ovoid, 330–600 × 230–400 μ, with poorly differentiated walls 25–35 μ thick, completely embedded at right angles to the surface in cushions consisting of loosely interwoven hyphae below with a thin cortex of brown pseudoparenchyma; asci cylindric to subclavate, 200–350 × 8–10 μ, with a 2.5–4 μ thick cap; ascospores filiform, multiseptate, breaking into 1-celled fragments 5–10 × 1.5–2 μ.

On larvae of Coleoptera in rotten wood. Illinois, *R. K. Benjamin*, ILL 21288. Maine, *R. Thaxter*, FH 6146. New York, *George H. Duff*, TYPE, FH 6132; *A. H. Smith 387, 425, 826* (MICH). North Carolina, *W. H. Wills* (MICH); *A. H. Smith 7393* (MICH). Tennessee, *R. Thaxter* FH 6144; *A. H. Smith 9861, 10169, 10543, 10772, 10834* (MICH). Washington, *A. H. Smith 19579* (MICH). Wisconsin, *R. A. Harper* (FH). Nova Scotia, *L. E. Wehmeyer 1213, 1213A* (MICH). Ontario, *A. H. Smith 4185, 26591* (MICH). British Honduras, *E. B. Mains 3837* (MICH).

This is a very variable species. The perithecia are embedded in lateral cushions, which may be well developed and partly surrounding the cylindric stromata (*C. viperina*, FIG. 40) or may be a few in irregular, very poorly developed cushions. In the latter the surrounding tissue is slight. Although the type of *C. viperina* shows considerable difference in this regard from that of *C. variabilis* there are specimens showing all degrees of variation between them. They are otherwise very similar and both have the characteristic furfuraceous condition.

30. CORDYCEPS UNILATERALIS (Tul.) Sacc. Syll. Fung. **2**: 570. 1883. (FIGS. 41–43).

Torrubia unilateralis Tul. Sel. Fung. Carp. **3**: 18. 1865.

Torrubia formicivora Schroet. Krypt. Fl. Schles. **3**(2): 276. 1894.

Cordyceps formicivora Sacc. Syll. Fung. **11**: 366. 1895.

Ophiocordyceps unilateralis Petch, Brit. Myc. Soc. Trans. **16**: 74. 1931.

Stromata slender, cylindric, acute to acuminate, 3–20 mm long, 0.2–0.5 mm thick, light to dark brown, tomentose, composed of compact longitudinal more or less interwoven brown hyphae, with a dense covering of brown multiseptate flexuous hairs, bearing one to several lateral or rarely terminal dark brown to brownish black pulvinate perithecial cushions 1.5–3 mm wide, rough from projecting perithecia; perithecia ovoid, 270–400 × 130–180 μ, very closely crowded, with ostioles opening on the outer surface of the cushion, with walls poorly differentiated, embedded except for the apices of the perithecia in a layer consisting of loosely to closely interwoven brown hyphae below covered with a thin cortex of brown pseudoparenchyma; asci clavate, 125–250 × 8–10 μ, with a 4–5 μ cap; ascospores somewhat fusoid, 100–162 × 2.5–3 μ, multiseptate with cells 5–14 μ long, not breaking into part-spores.

On ants, Hymenoptera, Formicidae. Illinois, *R. K. Benjamin,* ILL 21299. Maine, *R. Thaxter,* FH 4047, 4048, 6149, 6154. Michigan, *A. H. Povah 1368* (MICH). Mississippi, *M. E. Smith* (NY). North Carolina, *R. Thaxter,* FH 4057, 6161, 6190. Ontario, *H. S. Jackson* (MICH). Honduras, *J. Bequaert,* FH 6182, 6183.

The parasitized ants are often covered with a brown mycelium which attaches them to the substratum. The number and position of the perithecial cushions vary considerably (FIGS. 41, 42). They may be subterminal or terminal, the stromata thus appearing capitate. It is apparently this condition which Schroeter described as *C. formicivora* (Petch, **1937**; Mains, **1940a**).

Petch (**1924**, **1934**) has reported a conidial stage for *C. unilateralis* which he named *Hirsutella formicivora.* Specimen No. 6154 in the Farlow Herbarium bears conidia associated with perithecial stroma. The synnemata are 1.5–6 mm long, 0.3 mm thick, and light brown. The phialides are subulate, 12–20 μ long, 2 μ wide, gradually narrowing to acuminate apices. The conidia are ellipsoid or ovoid, 2–2.5 × 1–1.5 μ, without an evident mucus but adhering together in large numbers in clumps 14–60 μ in diameter. As has been pointed out elsewhere (Mains, **1951**), this differs from *Hirsutella formicivora* and the conidial stage therefore must remain doubtful until additional information is obtained.

31. CORDYCEPS SMITHII Mains, Jour. Elisha Mitchell Sci. Soc. **55**: 127. 1939.

Stromata capitate, 4–5 cm long, with narrow ovoid, reddish brown heads, acute above, with reddish brown tomentose stipes 0.2 mm thick, having a central core of longitudinal more or less interwoven hyaline hyphae and with a thin outer layer of brown pseudoparenchyma, the tomentum of the stipe consisting of dark brown multiseptate branched hyphae; perithecia ovoid, 240–260 × 140–160 μ, with poorly differentiated walls, with short periphyses lining the ostioles, closely crowded in a layer covering the head, completely embedded at right angles to the surface in a tissue consisting of outwardly interwoven hyaline or brownish hyphae with a brown cortex of pseudoparenchyma; asci clavate, narrowing toward the apices, 90–120 × 8–9 μ, with a 4 μ thick cap; ascospores fusoid, 60–100 × 2.5–3 μ, multiseptate, part-spores not seen.

On a wasp, Hymenoptera, Vespidae. Tennessee, *A. H. Smith 10396*, TYPE (MICH).

This species is known only from the type specimen. It is very different from other species known on wasps.

32. CORDYCEPS INSIGNIS Cooke & Rav. Grevillea **12**: 38. 1883. (FIG. 44).

Stromata clavate to subcapitate, 3–6 cm long, the upper perithecial portion obovoid or oblong, 12–15 × 6–8 mm, dark brown (mummy brown), the stipe 2–4 mm thick, cinnamon-brown, attached to the host by brownish rhizomorphs, with stipe and central core of the perithecial portion consisting of compact longitudinal hyaline to brownish somewhat interwoven hyphae; perithecia narrowly flask-shaped, 800–1000 × 250–320 μ, closely crowded, completely embedded at right angles to the surface in a layer covering the head of moderately interwoven brownish hyphae with a cortex of brown pseudoparenchyma and a palisade-like ectal layer up to 50 μ thick of parallel brown to hyaline hyphae; asci cylindric 600–700 × 5–6 μ, with a 4 μ thick cap; ascospores filiform, multiseptate, the cells 6–8 × 1.5 μ, part-spores not seen.

On larvae of an unidentified insect. North Carolina, *Mary Fitzgerald*, LH 41545 (BPI). Ohio, *C. R. Brewer*, LH 41537 (BPI).

Cordyceps insignis was described from a collection sent by Ravenel (*3251*) to Cooke from South Carolina. The species has been reported by Lloyd, who, however, confused it with *C. melolonthae* (Mains, **1958**). The species previously has been known only from the type specimen. Petch (**1934**) studied the type and the collections reported here agree very well with his data.

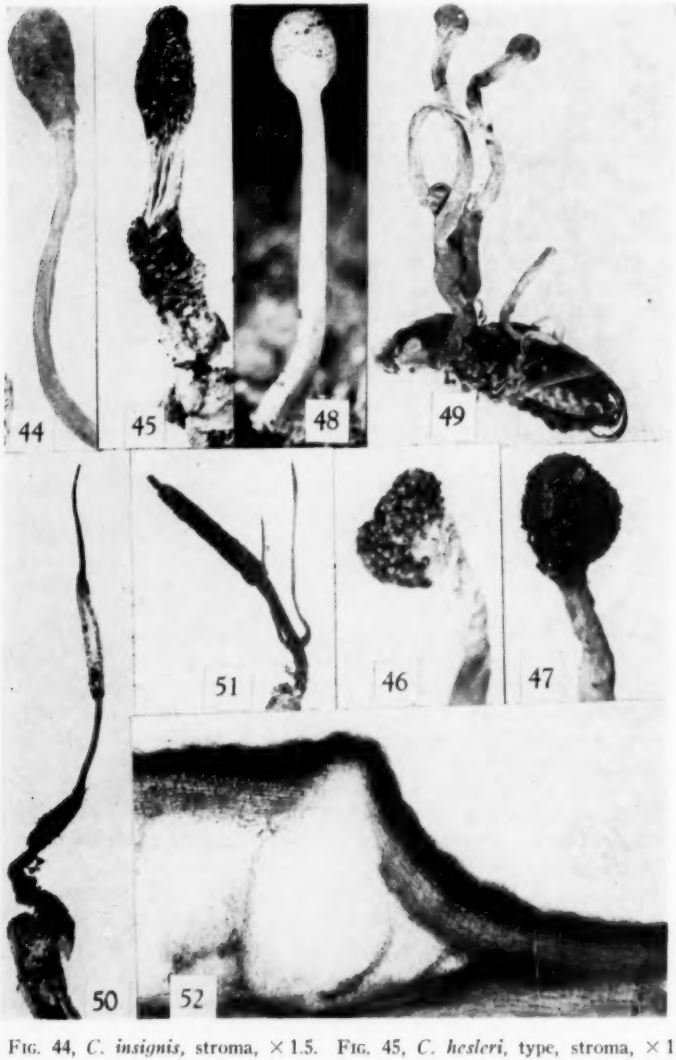


FIG. 44, *C. insignis*, stroma, × 1.5. FIG. 45, *C. hesleri*, type, stroma, × 1.8. FIG. 46, *C. entomorrhiza*, head of stroma, × 7. FIG. 47, *C. amazonica*, head of stroma, × 6. FIG. 48, *C. gracilis*, stroma, × 4. FIG. 49, *C. monticola*, type, stromata, × 2.4. FIGS. 50–52, *C. stylophora;* 50, stroma, × 1; 51, stroma with two conidial branches, × *2*; 52, cortex and perithecium, × 120.

33. CORDYCEPS HESLERI Mains, Journ. Elisha Mitchell Sci. Soc. **55**: 125. 1939. (FIG. 45).

Stromata clavate, up to 4.5 cm long, the upper ascogenous portion 7 mm thick, black, the stipe 5 mm thick, olivaceous gray, yellowish at base, with a central core of compact longitudinal somewhat interwoven hyphae, the stipe having a thin outer layer of very close interwoven brownish hyphae; perithecia ovoid, 650–960 × 350–420 μ, with a well differentiated brown wall up to 40 μ thick, completely embedded at right angles to the surface in a layer covering the upper part of the stroma consisting of outwardly loosely interwoven hyphae below and an outer cortical layer of dark brown pseudoparenchyma; asci cylindric, 300–360 × 6–7 μ, with a 3 μ thick cap; ascospores filiform, multiseptate, breaking into 1-celled fragments 3–4 × 1.5–2 μ.

On a cicada, Homoptera, Cicadidae. Tennessee, *L. R. Hesler 10939*, TYPE (MICH).

This species is known only from the type.

34. CORDYCEPS BELIZENSIS Mains, Mycologia **32**: 21. 1940.

Stroma capitate, 15 cm long, with a narrow ovoid head 20 × 9 mm, antimony yellow when fresh, yellowish brown dried, with a 2–3 mm thick stipe, straw-yellow stained with red when fresh, yellowish brown dried, with the stipe and central core of the head consisting of compact longitudinal somewhat interwoven hyphae; perithecia ovoid, 480–570 × 260–300 μ, with a well differentiated wall up to 25 μ, thick, completely embedded at right angles to the surface in a layer covering the head consisting of loosely interwoven hyphae below and having a 50–75 μ cortex of brownish pseudoparenchyma; asci cylindric, 200–300 × 5–6 μ, with a 2.5–4 μ thick cap; ascospores filiform, multiseptate, breaking into 1-celled segments, 4–8 × 1.5 μ.

On a larva of a Lepidoptera. British Honduras, *E. B. Mains 3687*, TYPE (MICH).

This species is known only from the type.

35. CORDYCEPS ENTOMORRIZA (Fr.) Link, Handbuch **3**: 347. 1833. (FIG. 46).

Sphaeria entomorrhiza Fr. Syst. Myc. **2**: 324. 1822.

Torrubia cinerea Tul. Sel. Fung. Carp. **1**: 61. 1861.

Cordyceps cinerea Sacc. Michelia **1**: 32. 1879.

Cordyceps carabi Quél. Comp. Rend. Assoc. Franc. Avanc. Sci. **26**(2): 452. 1898.

Stromata 3.5–4 cm long, capitate, the heads subspherical or obovoid, 2–3 × 2 mm, very verrucose, light vinaceous drab when fresh, the stipes

slender, 0.5–0.8 mm thick, pallid brownish and pruinose above, deep slaty brown and smooth below, the central core of the stipe and head consisting of compact longitudinal hyaline to brownish hyphae, the stipes having a thin outer layer of longitudinal dark brown hyphae; perithecia conoid to narrowly ovoid, 600–950 × 230–400 μ, crowded, with walls 25–35 μ thick, completely embedded at right angles to the surface in a layer covering the head consisting of loosely interwoven hyphae between the perithecia, with a cortex of brown pseudoparenchyma having an ectal layer of oblong hyaline to brownish cells; asci cylindric, 300–600 × 4–6 μ, with a 2.5–3 μ thick cap; ascospores filiform, multiseptate, breaking into 1-celled segments 6–10 × 1.5 μ; phialides produced in a compact palisade layer on the upper portion of the stipe, subcylindric to clavate, 12–16 × 2–2.5 μ, hyaline; conidia narrowly ellipsoid or fusoid, 5–8.5 × 2–3 μ.

On larvae of Coleoptera. Washington, *Mrs. Wm. B. Cooke,* A.H.S. 28906 (MICH). This is the only collection for North America, the species having previously been collected only in Europe.

There is considerable confusion concerning this species (Mains, **1951a**). The name has frequently erroneously been applied to *Cordyceps gracilis* and the species has been mostly reported as *C. cinerea.* Both *Stilbella setiformis* and *Hirsutella eleutheratorum* (Petch, **1933**) have been reported as the conidial stage but it is doubtful whether either is connected.

36. CORDYCEPS AMAZONICA Henn. Hedwigia **43**: 247. 1904. (FIG. 47).

Stromata 1–2 cm long, capitate, the heads ovoid or subgloboid, 3.5 × 3 mm, chestnut-brown, punctate from the ostioles, the stipes 1 mm thick ochraceous to purpuraceous, the stipes and central core of the head consisting of compact longitudinal somewhat interwoven brownish hyphae, the stipes bearing small clumps of interwoven hyphae; perithecia narrowly ovoid, 650–800 × 250–300 μ, with a brownish wall 15–20 μ thick, entirely embedded at right angles to the surface of the head in a layer covering the head consisting of loosely outwardly interwoven hyphae, with a cortex consisting of a thin layer, 15 μ, of brown pseudoparenchyma and an ectal palisade layer 25–30 μ thick of hyaline septate hyphae; asci cylindric, 180–210 × 4 μ; ascospores filiform multiseptate, breaking into 1-celled fragments 6–16 × 1 μ.

On cockroaches, Orthoptera, Blattidae. British Honduras, *E. B. Mains 3688, 3838* (MICH).

The specimens from British Honduras were over-mature and only a few asci in poor condition were seen. Petch (**1924**) has described a species *C. blattae* on cockroaches which differs in having clavate stromata, clavate asci without caps and fusoid ascospores which do not

break into fragments. The specimens from British Honduras agree very well with the description given by Hennings for *C. amazonica* on Locusta from Brazil. As discussed elsewhere (Mains, **1940b**) *C. amazonica* is not *C. locustiphila* Henn. as Petch has concluded.

37. CORDYCEPS GRACILIS Dur. & Mont. Fl. Algérie Crypt. 1: 449. 1846. (FIG. 48).

Stromata usually single, frequently with a dense growth of yellow mycelial strands around the host, 1.5–9 cm long, capitate, the heads globoid, ellipsoid or ovoid, 2–5 × 2–4 mm, mahogany red to ochraceous, punctate from ostioles of the perithecia, the stipes cylindric, 0.8–2 mm thick, deep chrome to straw yellow, the stipe consisting of compact longitudinal somewhat interwoven hyphae continuing into the head, diverging and becoming more interwoven; perithecia narrowly ovoid to conoid, 560–840 × 200–360 μ, completely embedded at right angles to the surface in a layer covering the head consisting of loosely woven hyaline hyphae below, becoming more densely interwoven above, with a cortex of brown pseudoparenchyma and an ectal palisade layer of hyaline to brownish hyphae 20–40 μ thick; asci cylindric, 400–528 × 4–6 μ, with a 4–6 μ cap; ascospores filiform, multiseptate, breaking into 1-celled fragments 6–8(–12) × 1–1.5 μ.

On larvae of Lepidoptera. Michigan, *M. Lange* (MICH); *A. H. Smith 3296, 15132, 18326* (MICH).

On larvae of Coleoptera, Elateridae. Illinois, *R. K. Benjamin* (MICH). Indiana, *H. W. Anderson* (NY). Michigan, *C. H. Kauffman* (MICH); *A. H. Smith 3966, 6375, 6419, 15099, 18951* (MICH).

Hosts uncertain. Florida, *W. A. Murrill* (NY). Michigan, *E. B. Mains 33–354* (MICH); *A. H. Smith 18847* (MICH). North Carolina, Curtis Coll. (FH).

Cordyceps gracilis has frequently been misidentified as *Cordyceps entomorrhiza* and it commonly occurs in herbaria under the latter name. *Cordyceps gracilis* has generally been reported on lepidopterous larvae. Möller (**1901**) reported it (as *C. entomorrhiza*) on a beetle larva. He noted the absence of mycelial strands and states that the perithecia are 900 μ long, the ascospores up to 660 μ and the part-spores 12 μ. Petch (**1933**) has concluded that Möller's fungus is *Cordyceps glaziovii*. Hennings (**1897**) described *C. glaziovii* as doubtfully on a lepidopterous larva and gives the perithecia as subglobose and the asci as 120–180 × 4–5 μ. Petch states that the type specimen is on a beetle larva but does not give a description of the *Cordyceps*, only stating that it "appears" to be the same as Möller's. Kobayasi (**1941**) has described a species, *Cordyceps gracilioides*, from Japan on larvae of Coleoptera,

which he distinguishes from *C. gracilis* mostly by lack of mycelial strands and larger perithecia, 830–900 × 200–280 μ and asci 600–700 × 6–6.5 μ. Accepting the description of Hennings, he also considers it distinct from *C. glaziovii*. These distinctions do not hold for North American specimens on beetle larvae. Specimens on lepidopterous and coleopterous larvae occur with and without mycelial strands. It does not seem feasible to recognize them as distinct species.

Isaria dubia Delac. has been reported (Petch, **1933**; Favre, **1942**) as the conidial stage of *Cordyceps gracilis* in Europe. This species of *Isaria* has not been reported from North America and a conidial stage has not been found in association with perithecial stromata.

38. CORDYCEPS MONTICOLA Mains, Mycologia **32**: 310. 1940. (FIG. 49).

Stromata 2–2.5 cm long, capitate, the heads subspherical to obovoid, 3–4 × 3 mm, brownish gray punctate from the dark brown ostioles, the stipes 1.5–2 mm thick, light gray, coalescing below, consisting of compact longitudinal somewhat interwoven hyphae; perithecia narrowly ovoid, 600–660 × 200–240 μ, completely embedded in the heads at right angles to the surface in a layer covering the heads of loosely interwoven hyphae below, with a cortex of thin brownish pseudoparenchyma, with an ectal palisade-like layer of hyaline hyphae 35 μ thick; asci cylindric, 420–510 × 5–6 μ, with a 4–5 μ thick cap; ascospores filiform, multiseptate, breaking into 1-celled fragments 6–8 × 1.5 μ.

On mole-cricket, Orthoptera, *Gryllotalpa hexadactyla*. Tennessee, *G. L. Williams*, TYPE (BPI).

This species is known only from the type specimen. A specimen on the same host from Louisiana was named *C. gryllotalpae* by Lloyd (**1920**). This only has very immature cylindric stromata with no evidence of a capitate condition.

II. SUBGENUS CORDYCEPS. SECTION 4. CYSTOCORDYCEPS

39. CORDYCEPS STYLOPHORA Berk. & Br. Jour. Linn. Soc. **1**: 158. 1857. (FIGS. 50–52).

Stromata usually single, slender, 1.5–4.5 cm long, the perithecial portion cylindric, surrounding the stroma, up to 2 mm thick, ochraceous tawny to dark cinnamon brown, with long acuminate sterile apices, the stipes 0.5–1 mm thick, concolorous, hirsute at the bases, pubescent above, the central core of the stipe, perithecial portion and the apices consisting of compact longitudinal hyaline to brownish hyphae, the outer longitudinal hyphae of the stipe dark brown, the stipe having scattered

short brown hyphal hairs; perithecia ovoid, 240–420 × 144–240 μ, with the wall up to 35 μ thick, hyaline within brown without, crowded, completely embedded at right angles to the surface in a layer consisting of loosely interwoven hyaline hyphae with a cortex consisting of compact longitudinal brown hyphae in continuation of the outer hyphae of the stipe; asci subclavate to subcylindric, somewhat attenuated above, 170–220 × 8–10 μ, with a 3 μ thick cap; ascospores filiform to narrowly subfusoid, 102–164 × 2–3 μ, multiseptate, the cells 12–20 μ long, not breaking into segments.

Conidial stage: *Hirsutella stylophora* Mains, Mycologia **43**: 702. 1951. Synnemata subulate, up to 4.5 cm long, 0.2–1 mm thick, brown; phialides preceding perithecial formation, sometimes on branches from stromata, hyaline, the lower inflated portions ellipsoid, 6–10 × 3–4 μ, narrowing above into acuminate sterigmata 8–12 μ long; conidia fusoid to obovoid, 5–8 × 2.5–4 μ, hyaline, covered with a slight mucus.

On beetle larvae, Coleoptera, Elateridae. Illinois, *R. K. Benjamin* (MICH). Michigan, *G. H. Hicks* (MICH, NY); *E. B. Mains 5054* (MICH); *A. H. Smith 7311, 7554, 7733, 11120, 32215* (MICH). New York, *George F. Atkinson*, CUP 8815, 9035; *H. J. Banker 1282* (CUP); *H. H. Whetzel*, CUP 14808; *A. H. Smith 395, 843* (MICH). North Carolina, *George F. Atkinson*, CUP 929, 10048. South Carolina, *S. C. Ravenel 1325*, part of TYPE, Curtis Coll. (FH). Tennessee, *A. H. Smith 10544* (MICH); *R. Thaxter*, FH 4055. Nova Scotia, *L. E. Wehmeyer 1167* (MICH).

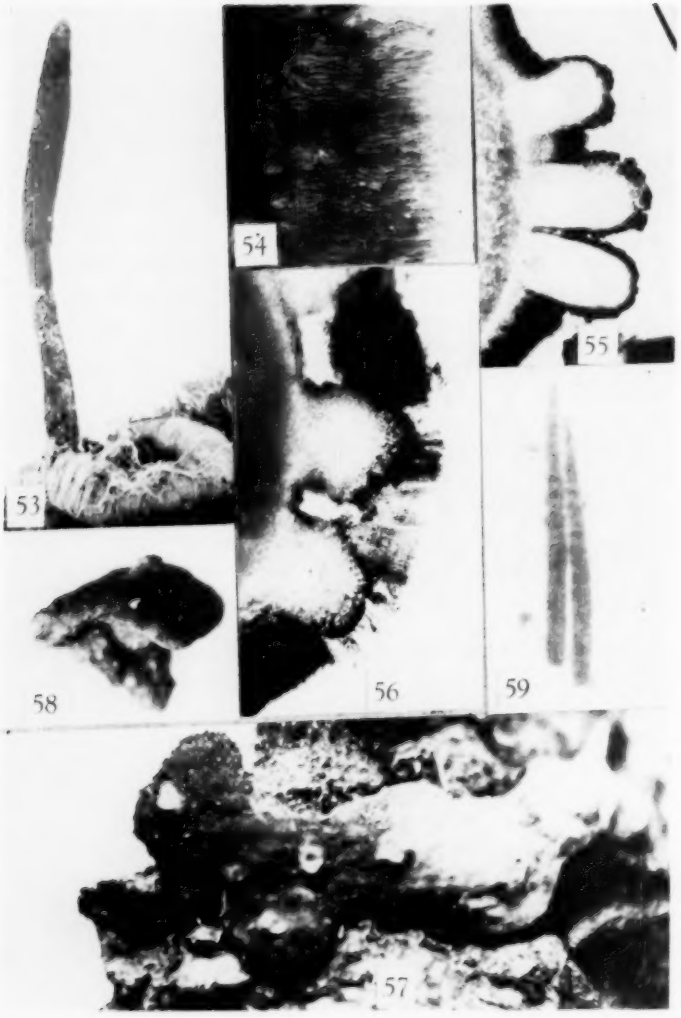
The structure of the perithecial stroma is unusual because the cortex is a continuation of the outer longitudinal hyphae of the stipe (FIG. 52). The perithecia probably are initiated within the longitudinal hyphae of the stromata and through their development split a layer off from the central core. The necks of the perithecia penetrate through the cortex to the outside and the spaces between the perithecia are filled with loosely interwoven hyphae.

The development of the stromata also is unusual, for, as shown elsewhere (Mains, **1941**), the stromata develop during late summer but do not mature until the next spring. This explains why many collections in herbaria are immature.

III. SUBGENUS CRYPTOCORDYCEPS

40. CORDYCEPS RAVENELII Berk. & Curt. Jour. Linn. Soc. **1**: 159. 1857. (FIGS. 53–56).

Stromata clavate, 4–10 cm long, the upper perithecial portion 3–5 mm thick, dark purplish brown to chocolate-brown, the apices usually sterile, the stipes 0.8–4 mm thick, the central core of the stipe and peri-



FIGS. 53–56, *C. ravenelii;* 53, stroma, × 1; 54, perithecial layer of palisade-like hyphae, × 300; 55, partly embedded perithecia, × 75; 56, perithecial layer partly torn loose by developing perithecia, × 75. FIGS. 57–59, *C. peltata;* 57, surface view of coalesced stromata, × 6; 58, stroma, × 7; 59, part-spores, × 1000.

thecial portion consisting of compact longitudinal somewhat interwoven hyaline to brownish hyphae, the stipes with a thin outer layer of longitudinal dark brown hyphae, the perithecial portion having a thin intermediate layer of brown pseudoparenchyma and an outer thick palisade-like layer of parallel dark brown hyphae at right angles to the axis of the stroma; perithecia hemispherical to subcylindric, 300–500 × 240–384 μ, brownish black, with the walls up to 60 μ thick, originating within the layer of pseudoparenchyma and pushing up through it and the palisade layer and projecting above it, sometimes pushing the palisade layer off and becoming free; asci somewhat fusoid or clavate, 175–336 × 7–10 μ, with a 2.5–3 μ thick cap; ascospores filiform, 132–252 × 2–2.5 μ, multiseptate, the cells 15–30 μ long, not or irregularly breaking into fragments; conidia narrowly obovoid, 5–7 × 2 μ, hyaline, 1-celled, produced on hyaline phialides scattered in the palisade layer.

On beetle larvae, Coleoptera, *Phyllophaga*, spp. Alabama, *C. G. Hollis*. Connecticut, FH 6186. Kentucky, LH 41279 (BPI). Massachusetts, *B. M. Davis* (MICH). Michigan, *M. Lange*, A.H.S. 25640 (MICH); *E. B. Mains 5062, 5090, 5325, 9501* (MICH); *A. H. Smith 15084, 15100, 15129, 15131, 15164, 15174, 18327, 36314, 51332* (MICH). New Hampshire, *R. Thaxter*, FH 2460, FH 3907, FH 6186, Rel. Farlow. 613. New York, *R. F. Pendelton* (CUP). North Carolina, *R. Thaxter*, FH 4050. Pennsylvania, *L. O. Overholts* (NY, BPI); *Everhart* (NY). South Carolina, *Ravenel 1272*, Curt. 3080, part of TYPE coll. (FH); Rav. Fungi Car. **4**: 28 (FH, NY, BPI). Tennessee, *A. H. Smith 10327* (MICH).

Petch (**1933**) has concluded that *C. ravenelii* is conspecific with *C. acicularis*, which has page priority. Berkeley cited Curt. No. 3080 (Rav. No. 1272) in the publication of *C. ravenelii*, and a specimen bearing these numbers occurs in the Curtis Collection of the Farlow Herbarium and apparently is part of the type collection. There is also in the Curtis Collection a specimen *Ravenel 1276* which is cited by Berkeley for *C. acicularis*. The two are very different species (see *C. acicularis*).

C. ravenelii is a unique species. The perithecia do not develop in a tissue of loosely interwoven hyphae as in other species with embedded perithecia. They appear to originate either in a thin pseudoparenchymatous layer or below it on the central core of longitudinal hyphae and develop through an outer palisade-layer (FIG. 54) and project beyond it (FIG. 55) or they may shove the palisade-layer off and become free (FIG. 56). The species has been described as having free perithecia but while some of the perithecia may finally become free, usually at maturity most or all are partly embedded in the palisade layer.

IV. SUBGENUS OPHIOCORDYCEPS

41. CORDYCEPS PELTATA Wakefield, Roy. Bot. Gard. Kew Bul. Misc. Inf. **1916**: 74. 1916. (FIGS. 57–59).

Ophiocordyceps peltata Petch, Brit. Myc. Soc. Trans. **16**: 74. 1931.

Stromata peltate with a short central umbo, 2–3 mm wide, 0.7–1 mm thick, vinaceous buff when immature becoming chestnut with vinaceous buff margins, punctate on the upper surface from slightly projecting ostioles of the perithecia, with short poorly developed stipes 1.5 mm wide above, narrowing below, completely embedded in the substratum, with stipe and head consisting of moderately to closely interwoven brownish hyphae becoming dark brown, closely interwoven above; perithecia narrowly ovoid, 430–480 × 168–204 μ, completely embedded vertically with ostioles opening on upper surface of the head, with a wall 10–15 μ thick; asci clavate, attenuated below, narrowing above, 176–192 × 9–11 μ, the wall not thickened into a cap; ascospores narrowly fusoid, 72–84 × 3–4 μ, multiseptate, breaking into half-spores at maturity.

On *Cryptorhynchus corticicolus*, Coleoptera. Barbados, FH 4046. The species was described from nearby St. Vincent in the West Indies.

This is a very unusual species. The wall of the ascus is not thickened at the apex into a cap. The ascospores at maturity break into multicellular half-spores (FIG. 59), a character which has not been reported for any other species of *Cordyceps*. The poorly developed stipes are entirely buried with the peltate heads resting on the substratum (FIG. 58). In the specimen in the Farlow Herbarium the heads have coalesced, giving an irregular crust-like appearance when viewed from above (FIG. 57). Lloyd (**1924**) has questioned the inclusion of this species in *Cordyceps*. It does not appear to be closely related to other species but seems to belong more properly in *Cordyceps* than in any other genus of the Hypocreaceae.

DOUBTFUL SPECIES

Cordyceps barberi Giard ex Massee, Ann. Bot. **9**: 18. 1895. Massee described and illustrated perithecial stromata on the sugar cane borer, *Diatraea saccharalis*, from John R. Bovell from Barbados and Antigua. Lloyd (**1916a**) states that the specimens from Bovell at Kew consist of sterile strands. There are two specimens in the Farlow Herbarium on the same host from Cuba and Puerto Rico determined as this species. Both are sterile.

Cordyceps fasciculata Pat. Bul. Soc. Myc. France **15**: 206. 1899. This species was described from a stroma on the pupa of an unidentified

insect from Guadeloupe. The type is in the Patouillard Collection of the Farlow Herbarium. The stroma is dark red, twice irregularly dichotomously branched. The perithecia are ovoid, 350–400 × 120–180 μ. They are closely crowded and appear to be embedded at right angles to the surface in a tissue of interwoven hyphae without a cortex. The asci are immature, Petch (**1933**) has suggested that this species may be the same as *C. polyarthra*. This is doubtful, as the latter has simple or rarely furcate stromata.

Cordyceps gryllotalpae Lloyd, Myc. Writ. **6**: 913. 1920. Lloyd published this name for a specimen on mole-crickets from Louisiana in the herbarium of the New York Botanical Garden. It consists of a number of very immature dark gray stromata. Kobayasi (**1941**) has decided that a *Cordyceps* on *Gryllotalpa* in Japan is the same. Collections agreeing with his description have not been seen from North America.

Cordyceps humberti Robin ex Saussure, Mon. Guêpes Soc. CLXIV, *pl. 5, fig. 9*. 1853–58. Very little is known concerning this species, which was described on wasps from Africa. Petch (**1934**) has decided that *Hirsutella saussurei* is the conidial stage of this species. A number of collections of this *Hirsutella* have been reported from North America (Mains, **1951b**) but without associated perithecial stromata. There is a collection in the Herbarium of the New York Botanical Garden under *C. sphecocephala* collected by A. G. Kevorkian, No. 181, in Puerto Rico which bears synnemata of *H. saussurei*. Accompanying the specimen is a photograph of a stroma having a cylindric perithecial layer and a sterile apex, as described by Petch for *C. humberti*. Unfortunately, the stroma is missing and additional information is not available.

Cordyceps palustris Berk. & Br. Jour. Linn. Soc. **1**: 159. 1857. This species was described from a specimen collected by Ravenel, No. 718, on the larvae of an unidentified insect in South Carolina. Petch (**1932**) states that part of this collection is in the herbarium of the British Museum but gives little additional information. The small, globoid (1.5 μ) part-spores and globoid perithecia may separate this from other species.

Cordyceps pittieri Bomm. & Rouss. Bul. Soc. Roy. Bot. Belgique **35**: 160. 1896. This species was described from a specimen on coleopterous larva from Costa Rica. The information given is not sufficient to establish its identity. Petch (**1934**) has suggested that it is *C. martialis* and Kobayasi (**1941**) has included it as a synonym of *C. melolonthae*.

EXCLUDED SPECIES

Cordyceps flavella Berk. & Curt. Jour. Linn. Soc. **10**: 375. 1869. This species was described from a collection of C. Wright, 519, from Cuba (Fungi Cub. Wright. 748). There is a specimen in the Curtis Collection of the Farlow Herbarium. It has several slender stromata from sclerotia in the inflorescence of some plant and is a *Claviceps*, as has been stated by Petch (**1933**).

Cordyceps montagnei Berk. & Curt. Jour Linn. Soc. **10**: 375. 1869. This name was applied to *Isaria gigantea* Mont. and a perithecial stage is unknown.

Cordyceps oncicada Westwood, Gard. Chron. **1891**, p. 553, *fig. 114B*. This species was reported on a cicada from an unknown locality—possibly Jamaica. From the illustration it apparently was very immature.

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EFFECT OF CARBOHYDRATES ON THE GROWTH OF CEPHALOSPORIUM LONGISPORUM IN A CHEMICALLY DEFINED MEDIUM [1]

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The genus *Cephalosporium* has assumed greater importance in recent years following the discovery of the production of antibiotics by some of its species (**2, 9**). With the exception of the study of Pisano, Olson and San Clemente (**7**) on the growth requirements of *Cephalosporium salmosynnematum*, a review of the literature reveals no detailed reports on the nutrition of this genus. Consequently, studies dealing with the growth requirements of *Cephalosporium* species were initiated in our laboratory. The present investigation concerns the utilization of 13 carbohydrates for growth by *Cephalosporium longisporum* in submerged culture.

MATERIALS AND METHODS

A chemically-defined, carbohydrate-free basal liquid medium based on the medium used by Pisano *et al.* (**7**) was employed in this study (TABLE I). A solution of the carbohydrate under test was sterilized separately and then added aseptically in 5 ml amounts to 45 ml of the basal medium so that the final concentration of carbon was equivalent to that amount of carbon (4 g/L) provided by one per cent glucose. Dextrin and soluble starch were employed at levels of one per cent. All media were contained in 250 ml cotton-plugged Erlenmeyer flasks. Only "Pyrex" brand glassware was used and it was washed in a synthetic detergent solution and rinsed successively in tap, demineralized and distilled water.

All flasks, including those used for the preparation of inocula, were incubated on a rotary shaker (Model V, New Brunswick Scientific Co.) which was located in an incubator maintained at 28.5° C. The shaker was operated at 250 rpm and had a one inch eccentricity. For the preparation of inocula, the growth from a slant of Czapek-Dox agar was suspended in 5 ml of sterile, distilled water and inoculated into a flask

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containing basal medium supplemented with one per cent glucose. The flask was shaken for 72 hours, following which the fungal growth was fragmented in a sterile blending apparatus for one minute at 8000 rpm. Five ml of a uniform cell suspension were used to inoculate a second flask of glucose medium. This flask was shaken for 24 hours; the fungal growth obtained was fragmented as above and then washed twice with sterile distilled water. One ml of the washed suspension served as the inoculum for each of a series of flasks of basal medium containing individual test carbohydrate. The inoculated flasks were incubated on the shaker. Duplicate flasks of each carbohydrate medium were removed from the shaker every 24 hours for five days, for measurement of pH and mycelial weight. The pH was determined with a Beckman model H2 pH meter. Mycelial growth was collected on tared filter papers (Whatman No. 1, 7.5 cm) by vacuum filtration. These were

TABLE I

COMPOSITION OF THE BASAL MEDIUM

Component	Concentration g/L
L-Glutamic acid	5.0
KCl	0.3812
$MgCl_2 \cdot 6H_2O$	0.3340
Na_2SO_4	0.4430
$NaH_2PO_4 \cdot H_2O$	0.8900
$ZnSO_4 \cdot 7H_2O$	0.0198
$FeSO_4 \cdot 7H_2O$	0.0248
$CuSO_4 \cdot 5H_2O$	0.0003

Distilled water to 900 ml.
pH adjusted to 7.0 with 2N NaOH.

dried in an oven at 100° C for 24 hours, allowed to cool to room temperature in a desiccator, and weighed on an analytical balance. Mycelial weights were calculated as grams per liter. Each experiment was run in duplicate with two separate trials for each carbohydrate. Weight determinations from four flasks of each carbohydrate varied less than ±12 per cent, and in most instances the variations were less than ±10 per cent.

RESULTS

Under the conditions of these experiments all of the carbohydrates studied, with the exception of lactose, were utilized to some degree by *C. longisporum*. From the mycelial weights obtained with each different carbon source it was possible to determine the time of greatest growth. In all cases, maximum yields occurred either at 24 or at 48 hours' incubation.

The average dry weights of mycelium obtained with each carbohydrate are reported in TABLE II. The control listed in this table represents growth obtained in carbohydrate-free basal medium. Of the pentoses studied, L-arabinose gave highest yields of mycelium at 24 hours' incubation with an average dry weight of 6.85 g/L. The enantiomorph, D-arabinose, on the other hand produced the greatest quantity of mycelium at 48 hours with a yield of 6.88 g/L. The hexoses investigated were D-glucose, D-mannose, D-galactose, D-fructose and L-sorbose. Of these, glucose and mannose gave peak yields of 7.77 and 7.19 g/L respectively at 24 hours' incubation. Glucose proved to be the most efficiently utilized of the carbohydrates studied. Good mycelial

TABLE II

GROWTH OF CEPHALOSPORIUM LONGISPORUM ON VARIOUS CARBOHYDRATES[2]

Carbohydrate	Hours of incubation				
	24	48	72	96	120
D-arabinose	3.91	6.88	6.27	5.46	5.35
L-arabinose	6.85	6.26	5.28	4.82	4.50
D-fructose	3.58	7.68	7.49	6.36	5.46
D-galactose	6.78	7.03	6.50	6.18	5.55
D-glucose	7.77	6.73	6.29	5.84	5.36
D-mannose	7.19	6.90	6.56	5.57	5.65
L-sorbose	2.87	5.40	5.23	4.54	4.49
Lactose	2.19	1.97	1.92	1.72	1.82
Maltose	7.12	6.05	5.78	4.96	4.84
Sucrose	6.85	6.05	5.18	4.86	4.72
Raffinose	6.97	6.39	5.61	4.83	4.84
Dextrin	2.37	1.96	1.84	1.70	1.58
Starch, soluble	2.32	2.32	1.94	1.74	1.66
Control[3]	2.12	1.88	1.79	1.62	1.51

[2] Growth is measured as dry weight and reported in grams per liter.
[3] Carbohydrate-free basal medium.

yields were obtained with fructose (7.68 g/L) and galactose (7.03 g/L) at 48 hours' incubation. With galactose, appreciable yields were already present at 24 hours. Sorbose was the most poorly utilized of the hexoses studied. With this sugar, 5.40 g/L of mycelium were obtained at 48 hours' incubation. Of the disaccharides studied, maltose gave the greatest growth (7.12 g/L), followed by sucrose (6.85 g/L) and lactose (2.19 g/L). Lactose was the poorest carbon source tested and values obtained with this carbohydrate were not significantly different from those obtained with the control. Greatest growth occurred with the disaccharides at 24 hours' incubation. Raffinose, which contains one mole each of D-fructose, D-glucose, and D-galactose, was the only trisaccharide studied. Each of the hexose components of this

sugar had been utilized by *C. longisporum*, as well as raffinose itself. Greatest growth was obtained with raffinose at 24 hours' incubation, the mycelial yield being 6.97 g/L. The good growth obtained with this sugar is of interest since reports in the literature, such as that of Volkonsky (**10**), record failure of utilization by a majority of fungi. The polysaccharides, dextrin and soluble starch, provided relatively poor sources of carbon for *C. longisporum*. Dextrin was utilized slightly more efficiently than starch, giving a dry weight of mycelium of 2.37 g/L at 24 hours' incubation, but by 48 hours autolysis of the mycelium had commenced. With starch, a yield of 2.32 g/L of mycelium was obtained at 24 hours and the same amount was recovered at the 48-hour harvest. In this instance, autolysis was detected within 72 hours.

No attempt was made to study adaptive enzyme formation with respect to carbohydrate utilization. If such enzymes could be induced, some of the mycelial weights obtained very likely would be of different magnitudes. In this connection, Perlman and O'Brien (**6**) recently reported being unsuccessful in their attempts to adapt a strain of *Streptomyces griseus* to utilizing sucrose or to fermenting sorbose by continued subculture of the organism in the presence of each of these sugars.

Changes in pH of the various carbohydrate test media were similar. In all instances the pH measured well over 7.0 after 24 hours' incubation. Where carbon sources were well utilized, pH values tended to be lower after 24 hours' incubation than when the carbon sources were more poorly utilized. As Hawker (**4**) has pointed out, if the amount of carbohydrate is low in media containing organic nitrogen, the fungus is compelled to obtain some of its carbon from the nitrogenous compound with the liberation of a large excess of ammonia. In this study, when the carbohydrates were poorly utilized by *C. longisporum*, and therefore largely unavailable, the fungus probably derived most of its carbon from the glutamic acid of the basal medium. Eventually, the pH in all test media rose to over 9.0, coincident with mycelial autolysis.

DISCUSSION AND CONCLUSION

C. longisporum was able to utilize a variety of carbohydrates when grown in a chemically-defined medium in submerged culture. The amount of growth varied with the carbon source and was determined by mycelial weight, a method of choice for measuring fungal growth. Multiple mycelial-weight determinations made throughout the incubation period revealed a more complete picture of the utilization of carbohydrates by this organism. Lilly and Barnett (**5**) have suggested that the ideal way to determine the growth potential of different sugars for

fungi is to measure the rate and amount of growth as a function of time of incubation. Since many studies in the literature dealing with the nutrition of fungi report growth measured at a single harvest period, the data obtained are necessarily incomplete and therefore subject to misinterpretation. This would be especially true if the weight determinations were made beyond the period of maximal growth and in the autolytic phase.

The rapid and substantial yields of mycelium obtained in this study emphasized the advantages of the submerged-culture technic over other methods of study of the nutrition of fungi, especially from the point of view of economy of time. When agar media or stationary liquid cultures are used, considerably longer incubation periods are required for maximum growth. Other advantages of submerged-culture methods have been adequately described by Foster (**3**).

The formation of large colonial masses in the test medium, rather than finely suspended growth, is an undesirable occurrence frequently encountered in submerged cultures. Foster (**3**) singles out the use of too small an inoculum as the major cause of large-colony formation, in that fewer cells are developing in a less competitive environment. In the present study, colonial-mass formation was avoided by fragmenting the culture in both stages of inoculum preparation. Large colonies were encountered only occasionally in the first stage of the preparation of the inoculum. Large colonies failed to develop when the growth from the first stage had been fragmented into smaller sized homogeneous particles and inoculated into a second flask.

Pridham and Gottlieb (**8**) and Benedict *et al.* (**1**) have employed the utilization of various carbohydrates by *Streptomyces* for the differentiation of species. It is conceivable that carbohydrate-utilization tests may be of value in distinguishing fungi of the genus *Cephalosporium*, notwithstanding the lack of uniformity of all isolates of a given species in utilizing a specific carbohydrate. Additional studies of carbohydrate utilization by species other than *C. longisporum* are necessary before the value of assimilation tests for this genus can be ascertained.

SUMMARY

1. *Cephalosporium longisporum* was able to assimilate 12 of 13 carbohydrates in a chemically-defined medium in submerged culture. Mycelial-weight measurements showed that glucose produced greatest growth of the fungus. The following carbohydrates were also utilized by *C. longisporum* and are listed in the order of decreasing effectiveness as carbon sources: fructose, mannose, maltose, galactose, raffinose, D-

arabinose, L-arabinose, sucrose, sorbose, dextrin and soluble starch. Lactose was not utilized to a significant extent.

2. Fragmentation of the culture in the preparation of the inoculum contributed to the reproducibility of the data.

3. The feasibility of the submerged-culture method as a technic for the study of the nutrition of fungi was demonstrated by studies with *C. longisporum*.

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PRODUCTION OF EXTRACELLULAR POLYSACCHARIDE IN CULTURES OF COCCIDIOIDES IMMITIS [1]

D. Pappagianis and George S. Kobayashi

(with 1 figure)

Filtrates from cultures of pathogenic fungi have been widely employed as serologic antigens, and in the detection of dermal hypersensitivity in the mycoses. Polysaccharides have been implicated as the antigenic (or haptenic) component of filtrates from the following fungi: *Coccidioides immitis* (Hirsch and D'Andrea, **1927**; Hassid *et al.*, **1943**); *Blastomyces dermatitidis* (Peck *et al.*, **1940**; Martin, **1953**; Dyson and Evans, **1955a**); *Sporotrichum schenckii* (Gonzales Ochoa and Figueroa, **1947**; Norden, **1951**); *Histoplasma capsulatum* (Scheff, **1945**; Cross and Howell, **1948**; Dyson and Evans, **1955b**); and *Blastomyces brasiliensis* (Fava Netto, **1955**). Most efforts to isolate these polysaccharides have resulted in preparations containing carbohydrate with 1 to 4 per cent nitrogen. In the case of *Coccidioides* polysaccharide, the nitrogen appears in amino acids (Pappagianis, **1955**). As yet it is not known whether the nitrogenous components accompanying the fungal polysaccharides are essential for serologic or immunologic activity.

The present work was concerned with some of the characteristics of extracellular soluble-polysaccharide formation by *C. immitis*. One of the objectives was to determine whether a relationship existed between the amount of polysaccharide and precipitin antigen formed [2] and virulence of the fungus.

MATERIALS AND METHODS

Three strains of *C. immitis* were studied. Strain Silveira and strain 46 have been described previously as being respectively of high and very low virulence for white mice (Pappagianis *et al.*, **1956**). Strain "Vene-

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[2] The term antigen and precipitinogen is used in this report with the understanding that only haptenic activity may be involved—i.e., the filtrates may be devoid of antigenicity.

zuela Brown" (VB) was a variant isolated from a strain submitted by Dr. Humberto Campins to Dr. Charles E. Smith, School of Public Health, University of California. The original culture had been obtained from a verrucous lesion on the knee of a woman in Venezuela. This variant was included because of its capacity to produce soluble extracellular substances which caused intense darkening of agar or liquid cultures. Its virulence was intermediate between that of strains Silveira and 46.

Mycelial growth and polysaccharide and precipitin antigen production by the three strains were followed in liquid medium. The medium employed was one slightly modified from the chemically defined synthetic asparagine medium of Smith *et al.* (**1948**) by the substitution of C.P. glucose for the U.S.P. grade "cerelose."[3]

In an initial experiment, designed to compare precipitin antigen production by strain Silveira and strain 46, cultures were grown in 700 ml amounts of the asparagine medium in "Low Form" culture flasks of 2500 ml capacity. Filtrates from these cultures were examined for precipitin reactivity after 10 weeks and 6 months static incubation at 34° C.

In a second experiment, strains Silveira, 46, and VB were compared with respect to formation of mycelium, polysaccharide, and precipitin antigen. Screw cap bottles of 200 ml capacity were used as culture vessels. Each bottle contained 100 ml of the asparagine medium and was inoculated with approximately 10^5 hyphal fragments from asparagine-broth cultures. Four cultures of each strain were removed from the incubator after 1, 2, 3, 4, 5, 10, and 18 weeks. The cultures were then treated as follows: The mycelial mats were removed by filtration, rinsed with ice cold distilled water, placed in individual Petri dishes and dried at 80° C for 18 hours. The dry mycelia were weighed and portions removed for nitrogen determinations. The filtrates were passed through Seitz filters and made up to 100 ml by addition of water and sufficient aqueous merthiolate solution to give a final concentration of 1:10,000 merthiolate. The pH of the filtrate from each culture was then measured with a Beckman H-2 pH meter. After the last (18 week) specimens were taken precipitin tests were carried out on aliquots of the filtrates, using pooled positive human serum and the method of Smith *et al.* (**1950**). A parallel series of precipitin tests was also carried out with strain-specific antiserum from monkeys infected with strain Silveira.

[3] Composition of medium, in g per 100 ml: glucose 1.0, glycerol 2.5, l-asparagine 0.7, NH_4Cl 0.7, K_2HPO_4 0.13, sodium citrate $5{\cdot}5H_2O$ 0.09, ferric citrate 0.3, $MgSO_4{\cdot}7H_2O$ 0.15, and distilled water.

Aliquots of 25 ml were removed from duplicate culture filtrates, dialyzed against running tap water for 72 hours and adjusted to 25 ml by pervaporation and addition of water.

Carbohydrate was determined by the anthrone method of Fairbairn (**1953**) with glucose as standard, although we have established that mannose appears to be the main component of the polysaccharide (Pappagianis, **1955**). The values resulting from the use of glucose as standard were lower than would be obtained with mannose. However, we do not feel that this detracts from the comparative merits of the data obtained for the three strains.

Nitrogen content was determined by the micro-Kjeldahl method (Hawk *et al.*, **1949**).

An attempt was made to ascertain the effect of varying the nitrogen source in the growth medium on the production of extracellular polysaccharide by strain Silveira. The four media tested contained the following nitrogen sources: Medium A, l-asparagine 0.1 per cent; medium B, NH_4Cl 0.1 per cent; medium C, NH_4Cl 0.35 per cent and l-asparagine 0.35 per cent; medium D, NH_4Cl 0.7 per cent and l-asparagine 0.7 per cent. Medium D is the asparagine medium used for coccidioidin production, and the nonnitrogenous components of these four media were as described by Smith *et al.* (**1948**). The pH of media C and D was 6.6, and media A and B were adjusted to this initial pH.

These media were dispensed in triplicate 700 ml amounts in "Low Form" culture flasks. Each flask was inoculated with approximately 10^6 arthrospores of strain Silveira and incubated at 34° for 2 weeks. The mycelial mats were filtered off and dried to constant weight as described above. The culture liquids were filtered and mertiolate added as before. The filtrates were concentrated about tenfold by pervaporation, then dialyzed for 72 hours against running tap water. The concentrated, dialyzed filtrates were adjusted to pH 3.0 with 1N HCl and centrifuged to remove the dark insoluble material which precipitated. Following neutralization of the concentrates to pH 7.0, alcohol-insoluble components were precipitated with five volumes of 95 per cent ethanol, washed with 95 per cent ethanol followed by acetone, and dried at 40° under reduced pressure. Carbohydrate determinations were carried out on these precipitates using the anthrone method.

RESULTS

Production of precipitinogen by three strains of C. immitis of different virulence. After 10 weeks' incubation, cultures of virulent strain Silveira showed the presence of precipitating antigen in undiluted fil-

trates, while similar filtrates from strain 46 were non-reactive with antiserum; and after six months strain Silveira filtrates still showed higher titers in the precipitin test.

In the comparison of the three strains, it was apparent that precipitin antigen was elaborated most rapidly by strain VB. Positive reactions were obtained with filtrates from two-week-old cultures of VB as shown in TABLE I. Strain Silveira gave positive-reacting filtrates at the third week, while strain 46 showed no precipitinogen until the fourth week of incubation. TABLE I also shows the higher titer attained in filtrates of VB after 10 weeks. After 18 weeks incubation the three strains gave positive reactions at a dilution of 1:100. These results were obtained with pooled human serum and were essentially the same as those obtained with serum from monkeys infected with strain Silveira.

TABLE I

FORMATION OF SEROLOGICALLY ACTIVE CULTURE FILTRATES BY THREE STRAINS OF COCCIDIOIDES IMMITIS

Strain	Dilution of filtrate								
	0			1 : 10			1 : 40		
	46	Silv	VB	46	Silv	VB	46	Silv	VB
Age of culture, weeks									
1	–	–	–	–	–	–	–	–	–
2	–	–	++++	–	–	–	–	–	–
3	–	++++	++++	–	–	++++	–	–	–
4	++++	++++	++++	–	–	++++	–	–	–
5	++++	++++	++++	–	–	++++	–	–	–
10	++++	++++	++++	–	++++	++++	–	–	++++
18	++++	++++	++++	++++	++++	++++	++++	++++	++++

It appeared, therefore, that the precipitating antigens were not strain specific.

Relative rates of growth and of formation of extracellular polysaccharide and nondialyzable nitrogenous components. For the first 3 to 4 weeks, little difference could be discerned macroscopically in the yield of mycelium by the three strains. It was apparent, however, that the culture liquid of strain VB was darkening more rapidly. By the tenth week VB filtrates and those from Silveira cultures were intensely darkened; and by the eighteenth week, VB filtrates were the color of molasses and virtually opaque to daylight. Silveira filtrates became dark brown and strain 46 produced light brown filtrates.

Mycelium dry weight, polysaccharide formation, and changes in pH during growth of the three strains are shown in FIG. 1. There was

an initial period of growth for the three strains which continued through the fourth week. During the fifth week there was a decrease in mycelial weight and this decrease was even more profound when cultures were examined after 10 weeks. However, by the time the final cultures were examined after 18 weeks of incubation, strains Silveira and 46 showed a large secondary increase in mycelial weight while Strain VB recouped only half the earlier loss in cell yield.

Concomitant with the decrease in cell weight in VB cultures and the increased darkening of the medium was an obvious deterioration of the mycelium, which lost its turgidity and became slimy and incoherent.

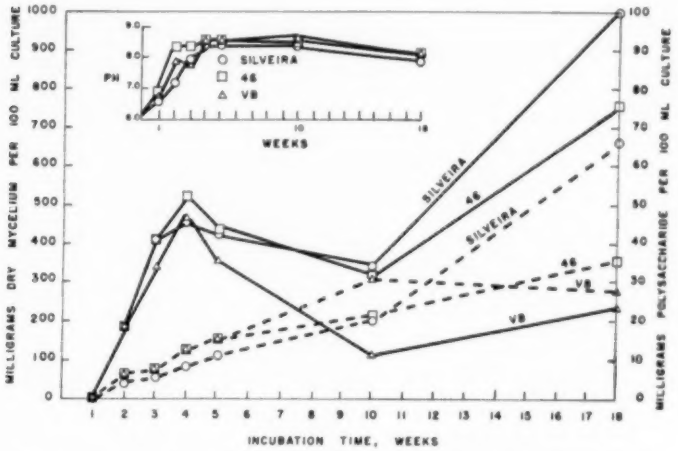

FIG. 1. Comparative yield of mycelium and extracellular polysaccharide by three strains of *Coccidioides immitis*. Inset shows variation of pH in cultures. (——— = Mycelial dry weight; - - - - - = polysaccharide.)

It was apparent that autolysis was extensive. The mycelial mats of strains Silveira and 46 retained the dry appearance of aerial hyphae on their upper surface. However, the undersurface was mucoid, and microscopically the hyphae were virtually empty and showed only occasional masses of intracellular substance.

The rate of formation of extracellular polysaccharide as shown in FIG. 1 indicated a steady rise in polysaccharide liberation from the second through the fifth week and appeared even higher at the tenth week of incubation. The cultures of strain VB at 18 weeks showed no increase in polysaccharide over the yield at 10 weeks. Accompanying

the secondary increase in yield of Silveira mycelium was an almost parallel increase in polysaccharide. The secondary growth of strain 46 was not accompanied by an increase in rate of polysaccharide formation.

The pH changes observed in the filtrates have been plotted in FIG. 1. Cultures of the three strains showed a similar rise in pH from 6.2 to 8.5 in the first five weeks, and persistence at this alkaline level until the last phase of incubation (10 to 18 weeks), during which a slight depression in pH took place.

In TABLE II are shown the amounts of nondialyzable nitrogen obtained in the filtrates. In filtrates of strain 46, there was only a slight increase in nondialyzable nitrogenous materials after the fourth week.

TABLE II

FORMATION OF EXTRACELLULAR, NONDIALYZABLE NITROGENOUS MATERIALS BY STRAINS OF COCCIDIOIDES IMMITIS AND RATIO OF POLYSACCHARIDS TO NONDIALYZABLE NITROGEN

Age of culture, weeks	Strain					
	Silveira		46		VB	
	CHO* / N	N, μg per ml	CHO* / N	N, μg per ml	CHO* / N	N, μg per ml
1	0.78	14.4	0.86	9.5	0.96	7.3
2	0.86	18.2	3.16	8.4	1.94	11.2
3	1.63	30.7	4.88	11.5	3.71	15.0
4	2.54	35.2	6.77	17.9	6.73	18.4
5	2.84	39.8	9.87	16.4	7.19	23.8
10	3.50	57.9	11.42	21.1	6.43	48.2
18	8.85	74.6	16.69	21.9	5.29	50.9

$$\text{Ratio} = \frac{\text{mg glucose equivalents}}{\text{mg N}}.$$

Strain VB appeared to produce these substances at least through the tenth week, but by the eighteenth week had accumulated only slightly more. Strain Silveira continued to liberate large-molecular nitrogenous substances through the eighteenth week. The yield of nondialyzable nitrogenous substances by the three strains corresponded to their differences in virulence—i.e., Silveira greatest, VB second, and strain 46 lowest.

The data in TABLE III clearly reflect that the ratio of polysaccharide to nondialyzable nitrogenous products underwent great changes; and there were considerable differences among the strains with respect to output of polysaccharide and nitrogenous materials, possibly proteins.

Influence of asparagine and ammonium chloride as nitrogen source on mycelial growth and on the formation of extracellular polysaccharide. Visible growth of strain Silveira was observed in three days in media C and D, but was delayed 9 or 10 days in media A and B. Furthermore, the gross morphology was markedly different in the four media. The average yield (dry weight) of mycelium and final pH of the various media are shown in TABLE III.

The comparative yields of polysaccharide with varying nitrogen supply shown in TABLE III indicated that medium A gave the largest amount of polysaccharide per gram of cells though the yield of mycelium

TABLE III

YIELD OF SOLUBLE POLYSACCHARIDE AND MYCELIUM OF COCCIDIOIDES IMMITIS GROWN IN SYNTHETIC MEDIA WITH VARIATION IN NITROGEN CONTENT

Medium	Nitrogen source, per cent	Flask	Final pH	Dry wt. of cells, g	Total soluble non-dialyzable solids, g	Polysacch. per gram dry cells, g	Polysacch. per ml of medium, mg
A	Asparagine 0.1	1	7.60	1.7	0.9871	0.1332	0.323
		2	7.65	2.1	0.6680	0.0844	0.253
		3	7.70	2.1	0.9715	0.1059	0.318
B	NH_4Cl 0.1	4	3.30	Sample lost			
		5	3.30	2.7	0.2007	0.0188	0.073
		6	3.25	2.9	0.1262	0.0098	0.040
C	NH_4Cl 0.35 Asparagine 0.35	7	7.50	4.45	0.8419	0.0595	0.394
		8	7.10	4.60	0.7133	0.0513	0.337
		9	6.80	4.9	0.8005	0.0603	0.422
D	NH_4Cl 0.7 Asparagine 0.7	10	7.65	5.87	0.8142	0.0559	0.469
		11	Sample lost				
		12	7.60	6.9	0.4182	0.0220	0.217

was lowest in this medium. Medium B gave the lowest yield of polysaccharide, one-tenth to one-quarter of that recovered from medium A. Medium C and D gave the largest yield of mycelium, but the polysaccharide yield only slightly exceeded that of medium A.

DISCUSSION

The production of soluble extracellular polysaccharide by these strains of *C. immitis* may be accompanied by complex changes in the growing cultures. It is evident that nonhomogeneity is a characteristic of some mold cultures with surface mycelium, since a portion of the mycelium may be physiologically active and growing, while another part

may be undergoing autolytic degeneration (Schmidt, **1936**). The highest amount of polysaccharide at 10 weeks was found in VB cultures which also showed the highest titer in precipitin tests. The time of maximum content of polysaccharide in VB filtrates corresponded to the time at which mycelium weight had reached its lowest level and nondialyzable nitrogenous substances were maximal in the filtrate. This would appear to support the idea that polysaccharide was liberated by autolysis. However, the occurrence of secondary growth with strains Silveira and 46 obscures such a conclusion with these strains. A secondary growth was previously reported by Smith *et al.* (**1950**) for mixed cultures of *C. immitis*. With such complex changes taking place in static mold cultures, it is perhaps not surprising that great variation has been encountered in coccidioidin preparations (Smith *et al.*, **1948**; **1950**).

Two notable effects were encountered with modification of the nitrogen source. First, the yield of polysaccharide per gram of dry cells was greater under conditions of nitrogen limitation. Second, the yield of polysaccharide was greatly depressed by the use of NH_4Cl as the source of nitrogen. This was possibly related to the low pH resulting from the utilization of NH_3. It appears from the earlier experiments that autolysis with release of polysaccharide may be encouraged by greater alkalinity. In the work of Behr (**1930**) and Schmidt (**1936**), it was evident that autolysis of *Aspergillus niger* increased with alkalinity of the medium. While it might be expected that autolysis would liberate polysaccharide and nondialyzable nitrogenous substances in a constant ratio, the values obtained were extremely variable. This may be due to variable proteolytic activity among strains.

The demonstration of quantitative variability in the liberation of extracellular materials including antigens (haptens?) by different strains of *C. immitis* is of practical significance. Perhaps this contributes to the variable times at which coccidioidins can be harvested from multiple-strain cultures. There is no indication, however, of a qualitative difference in the immunologically important extracellular substance of different strains of *C. immitis* (Smith *et al.*, **1948**; Pappagianis, **1955**).

A relationship between polysaccharide production and virulence was sought on the basis of the significance in virulence of various soluble polysaccharides—e.g., the pneumococcal polysaccharides, soluble levans (Hestrin *et al.*, **1954**) and antiproperdin polysaccharides (Pillemer *et al.*, **1955**). From the present studies it cannot be stated that virulence is correlated with the quantity of polysaccharide liberated by *C. immitis*. On the other hand, the release of nondialyzable nitrogenous substances was proportional to the virulence of the three strains studied, but the possible significance of this finding is presently unknown.

The importance of autolysis in the liberation of polysaccharide and antigens of *C. immitis* has received support from the recovery of precipitin and complement-fixing antigens after induction of autolysis of *C. immitis* (Pappagianis *et al.*, **1957**). A polysaccharide similar to that from culture filtrates was also obtained in the induced autolysates.

SUMMARY

Three strains of *Coccidioides immitis* which differed in virulence for white mice were studied with regard to growth rate and output of polysaccharide, nondialyzable nitrogenous substances and precipitinogen over an 18 week period. The three strains had a comparable growth rate over a 4 week period followed by a loss in mycelial weight between the fourth and tenth weeks. This loss in weight occurred concomitantly with the attainment and maintenance of maximum alkalinity, pH 8.4 to 8.7, and was most profound with strain "Venezuela Brown" (VB) which underwent extensive autolysis. The other two strains manifested a striking secondary growth between the tenth and eighteenth weeks. There appeared to be no correlation between virulence of the strains and production of extracellular polysaccharide, while the liberation of nondialyzable nitrogenous substances appeared proportional to virulence. The formation of precipitinogen was most rapid in cultures of strain VB of intermediate virulence. The release of extracellular polysaccharide appeared to be greater under conditions of nitrogen limitation. The low pH in the growth menstruum resulting when NH_4Cl was the nitrogen source appeared to restrict the output of polysaccharide.

The possible significance of autolysis in the release of antigens by *C. immitis* was discussed.

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MYCOLOGICAL INVESTIGATIONS ON TEONANÁCATL, THE MEXICAN HALLUCINOGENIC MUSHROOM.[1]

PART I. THE HISTORY OF TEONANÁCATL, FIELD WORK AND CULTURE WORK

ROLF SINGER

(WITH 6 FIGURES)

1. HISTORY

The use of hallucinogenic mushrooms in Mexico was reported by European and Mexican writers (**11**) centuries ago, and so is not news. Nor are mushrooms unique as hallucinogens. It is widely known that peyotl, *Lophophora williamsii* (Lem.) Coulter, a cactaceous plant likewise native to Mexico, contains a hallucinatory substance, mescalin. What is new in recent developments is the serious attempt to study the organisms responsible for these curious phenomena, an endeavor logically beginning at the biological level—*i.e.*, with a study of the mycological aspect of the rather complex problem. With this goes an attempt to obtain more details on the ethnobotanical role of the hallucinogenic mushrooms in southern and central Mexico. A consequence, and, to a certain degree, also a motive, of all this renewed interest in the subject is the extraction in pure form of a substance or substances important in medical research, or at least data on the active principle in these fungi which might throw light on phenomena of practical concern, such as the symptoms commonly referred to as schizophrenic, or the question of the maturity factor in neuroses.

Before the first specimens had come to the botanical laboratories, there had been some doubt whether the *teonanácatl* of the literature, a word supposedly meaning "sacred mushroom" in the Aztec language, was actually a mushroom rather than *Lophophora*. The word *teonanácatl* is here used in the sense of Schultes (**13**), Heim, and in fact the majority of the authors concerned with hallucinogenic mushrooms in

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Mexico (**3**, **10**, **11**, **12**, **18**, **19**)—*i.e.*, as a general term for any hallucinogenic mushrooms used by Mexican Indians in pre-Columbian times and up to the present. While botanical interpretations of the word *teonanácatl* were originally based on Schultes's (**13**) paper, and referred to one single species of *Panaeolus*, we shall see subsequently that *teonanácatl* is not necessarily a single species, and that it is not—according to our present knowledge—probable that *Panaeolus* spp. are represented in the list of hallucinogenic mushrooms in Mexico.

Actually, the first correct interpretation of *teonanácatl* was published by this writer in 1951 (**16**, pp. 472, 506). This fact has not been mentioned in the current literature, although the genus *Psilocybe* as well as the species *Ps. cubensis* was mentioned by me in the place quoted. These indications were based on material collected by Dr. R. E. Schultes of Harvard University.

Schultes undoubtedly deposited the first botanically useful specimens of hallucinogenic mushrooms from Mexico in an American herbarium. These consisted of two collections, originally placed on one sheet in the Farlow Herbarium, but later separated by the present author (1941). One package containing *Panaeolus* was determined by D. H. Linder, then Curator of the Farlow Herbarium, as *Panaeolus campanulatus* var. *sphinctrinus*. If we disregard questions of nomenclature (the rules of botanical nomenclature necessitate a change in the name used by Linder, to read "*Panaeolus sphinctrinus* (Fr.) Quél."), we may say that Linder's determination is correct. Heim (**3**) came to the same conclusion. But even though the determination is correct for these specimens, it is obvious from certain data on the label of the collection [2] that there must have been some confusion of the *Panaeolus* with what later became known as *Psilocybe mexicana*, while on the other hand further inquiries show that *Panaeolus* is not one of the genera used by Mazatec Indians of the Huautla region for either religious or medical purposes.

The other package, originally inserted with the first, remained un-

[2] The label reads in part: "Springy meadows in rainy season. Huautla de Jiménez, Oaxaca, Mexico, July 27, 1938. Stem 1–2 mm diam., 10 cm high; hemispherical but often cuspidate; gills dark brown-black, whole plant coffee brown, black when dry. Mexican name nanacate. Indian name: she to (eruption of the earth); tso-ska (loco mushroom). Said to be poisonous in overdose of 50–60, but in moderate quantity it produces hilarity and general narcotic feeling of wellbeing for an hour. Excess doses said to produce permanent insanity. . . ." It is now evident that "springy meadows" are the characteristic habitat of *Psilocybe mexicana*, and it is this species that is "cuspidate," never *Panaeolus sphinctrinus;* dark brown lamellae would be characteristic for the former, black ones for the latter. The name *she to* is a misspelling of *xi-tjo*, which is the general word for mushrooms and fails to identify the genus.

named in the Farlow Herbarium until this author in 1941 determined it as *Psilocybe cubensis* (Earle) Sing. (at that time still as "*Stropharia caerulescens* (Pat.) Sing. = *Stropharia cubensis* Earle"). Strangely enough, this second collection by Schultes contains a note in which the local name of the species is indicated [3] as *kee-sho*, which in Huautla does not refer to the species represented by the dried carpophores in the

FIG. 1. Map of central and part of southern Mexico, between the 18th and 22nd parallels, showing Amecameca, Tenango, and Huautla in their respective states. 1:7,500,000.

package, but to *Psilocybe caerulescens* Murr., as we shall see later. The specimens and data come from the not very accessible Mazatec village Huautla, the same village where the *Panaeolus sphinctrinus* had been

[3] The label of this specimen reads: "Plantae Utiles Mexicanae. Oaxaca. Botanical Museum, Harvard University. Common name (Mexican) nanacate. Tribe: Mazatec. Indian name kee-sho. Habitat in freshets during rainy season. Locality Huautla de Jiménez, Oaxaca. Uses: From four to eight are eaten to produce a temporary narcotic state of hilarity. Said to be poisonous if taken in excess, causing permanent insanity. [Next follow descriptive data, illustrated by a drawing on the reverse side.] Coll. no. 349. Coll. Richard Evans Schultes, 27 July, 1938." Below Schultes's name that of Blas Pablo Reko is added (as co-collector). On a separate label, there is an annotation by Singer: "*Stropharia caerulescens* = *Psilocybe cubensis* (Earle) Sing.," and the Farlow label was made out correspondingly, although here the second and valid name was omitted. Thence resulted a later erroneous reinsertion in *Stropharia* when the herbarium material was shifted between 1949 and 1951, under W. L. White, curator.

collected, and where, later on, by Wasson, Heim, and Singer, *Ps. caerulescens* was likewise found (FIG. 1). If we assume that *Ps. mexicana* was originally confused with *Panaeolus sphinctrinus,* and *Ps. caerulescens* with *Ps. cubensis,* by Schultes's source of information, we already have all three important hallucinogenic mushrooms of the Mazatecs, or rather traces of them, in the first two records. These psilocybes will later be treated in more detail.

This was the status of the mycological knowledge of *teonanácatl* when in 1952 Dr. Sam I. Stein became interested in the psychiatric implications of certain reports on the action of such dark-spored agarics as *Psilocybe* and *Panaeolus* (**1, 2, 6, 9, 10, 11, 12, 13, 16**). He then began to prepare the organization of a research program on fungus toxicology as related to neuropsychiatric problems. One of the first steps planned was the collection of dried material and cultures of the respective species, and of botanical observations made on the spot. These were not only to help in solving the basic problem from a biological point of view, but to produce sufficient knowledge to grow fruiting bodies of these species in the United States, or to grow mycelium in sufficient quantities to satisfy the demands of further investigations. The origin of these cultures had to be carpophores from the now classical village of Huautla de Jiménez, since obviously only a mushroom population known by previous tests and observations to be hallucinogenic should become the starting point of the production of carpophores destined to be the raw material for further experiments—particularly bio-assays and biochemical analyses—in the investigation on hallucinogens. This localization does not exclude further search for different species used in some remote valley of Mexico or Guatemala, or elsewhere.

The first author to publish data on chemical analysis and animal tests was Santesson (**12**), who unfortunately was handicapped by lack of thorough botanical study of the material he used, and by the application of inadequate chemical and experimental procedures. He had two samples, one "probably belonging to a *Panaeolus,*" and the other supposed to be *Armillariella mellea* (although that was neither clear from the text nor at all probable). It is more likely that the material consisted of *Psilocybe mexicana* and *Ps. cubensis,* but it may conceivably have been a mixture of numerous elements. It was referred to as *teonanácatl.* Chemical reactions supposedly showed that no alkaloid was involved. According to the Fehling reaction, Santesson's material seemed to contain a glucoside as the active principle. Subcutaneous injections of 2.12 g and 1.57 g of the drug per kilogram body weight of *Rana temporaria* resulted in a "semi-narcosis" of the frogs, with a nega-

tive "turning test" (the classical inhibition effect of morphine on the rotation reflex of frogs).

At the time I reached Mexico—*i.e.*, one year after Heim had accompanied the Wassons there—the former had already published three short communications (**3, 4, 5**) on specimens of Mexican species believed to be used in Indian ceremonies, and a preliminary article on his own observations. The name *Psilocybe mexicana* was then proposed for the first time, although not validly published before the second half of 1957. For what we consider to be *Ps. caerulescens* Murr., Heim proposed a new name, *Ps. mazatecorum*,[4] and having traveled to regions further south and northwest, he added a number of new entries on the list of species which collectively may be termed *teonanácatl*. Among them was *Ps. zapotecorum* Heim, from the Sierra Costera, and *Ps. aztecorum* Heim, from Popocatépetl. Fair to excellent illustrations of these species were provided by Heim for the Wassons' article (**19**) and in their book (**20**). In both of these latter publications as well as in other articles, ceremonies conducted by local curanderos (and a curandera) and experiences under the influence of hallucinogenic mushrooms were described by the Wassons and Roger Heim. No results of chemical analyses or animal tests have been published as this is written. Nevertheless, the attention given the mushrooms in the press has created—far beyond Mexico—an extraordinary interest and expectancy. Whether this attitude is justified by the research now in progress remains to be seen.

2. FIELD AND CULTURE WORK IN 1957

My journey from Mexico City to the Mazatec country was undertaken in the company of two young Mexican botanists, M. A. Palacios, who worked as my assistant, and G. Guzmán H., an ardent student of agarics. There could not have been better traveling companions, or ones who better served the purpose of the trip.

We reached Huautla the first week of July and were there the guests of an Indian family. The head of the family, Isauro Nava García, an exceptionally intelligent and cooperative man who could express himself well in Spanish, and equally well spell the words of his native Mazateco, turned out to be a keen observer of fungi. He recognized easily and almost infallibly the different species of *Psilocybe*, knew where they could be found and when, and pointed out the interesting features of their re-

[4] After having been advised by Dr. Alexander H. Smith of the probable identity of this fungus with Murrill's type of *P. caerulescens*, Heim changed the name to *P. caerulescens* var. *mazatecorum* Heim, because, as he explains, of the high variability of these fungi.

spective habitats. He was of course completely familiar with the mushroom lore of his valley and had eaten hallucinogenic mushrooms before. Either he or his brother-in-law accompanied us in many of our collecting trips. Everything he said was checked by comparison with information obtained elsewhere. All the data obtained from him were corroborated with the exception of an opinion about the activity of a mushroom called "nčhe-je nčhe-je" (now known as *Ps. candidipes*), which was variously called inactive and poisonous. This, by the way, is the only species of the taxonomic group to which the hallucinogenic psilocybes belong that was not likewise reported by Wasson and Heim from the Mazatec region. On the other hand, the species said to be hallucinogenic and not belonging in the same taxonomic group as *Ps. cubensis, mexicana,* and *caerulescens* were not confirmed as hallucinogens by our own inquiries and observations. These unconfirmed data (**3**, **4**, **16**) refer to *Conocybe siligineoides* Heim, two species of *Panaeolus* (*P. sphinctrinus* and *P. fimicola* sensu Heim), and those psilocybes not reported to show any blue discoloration or stain (*i.e., Ps. cordispora* and *Ps. macrocystis*). I may add that there are a *Psathyrella* and copelandias from Santa Cruz which Guzmán, who collected them there, is inclined to think may be hallucinogenic. When we met Mr. Wasson in San Andrés near Huautla, he suggested that among these species the chances of finding real hallucinogens are rather good in *Conocybe*. So they are also in *Panaeolus* and related genera, since species of these have been shown to be poisonous or inebriating, and to be active in animal tests—*e.g., Panaeolus venenosus* Murr. (**9**), which is apparently a synonym of *P. subbalteatus,* and species of the same genus or related genera determined in the past as *Panaeolus papilionaceus* and *P. "campanulatus."* Unfortunately, some of these determinations (**1**, **2**, **6**) may not be accurate and may just as well refer to other related genera (*Anellaria, Copelandia*), or at least to other species. We must insist, however, that the phenomena which belong in the class of "cerebral mycetisms" in the terminology of Ford (**2**) are not fully identical—although comparable—with the hallucinatory-euphoric and lasting effect described for the psilocybes. Aside from that we feel certain that *Panaeolus sphinctrinus* is not used as a drug by present-day Indians in Mexico.

As for *Conocybe siligineoides*—which would be the only forest-inhabiting, or even xylophilous, species among those indicated by any author, it will be well to take into consideration a statement made to us by Isauro Nava. He said that there was, growing at a certain distant locality and not fruiting at the time of our visit, another hallucinogenic mushroom, as small as "pajaritos" (*Psilocybe mexicana*) and of the same shape and also staining blue, but differing in its habitat—wood in

the forest rather than soil of meadows. Just such a species (*Ps. yungensis*) had been collected by me a year earlier in the ecologically very similar Bolivian Yungas, also a tropical-montane forest, and a similar but different one (*Ps. pelliculosa*) by Alexander H. Smith in the Pacific Coast area of the United States in coniferous forests of a temperate type. It is therefore quite possible that the missing forest-inhabiting hallucinogenic mushroom is not the species described by Heim as a *Conocybe*, but another representative of the section in which all the other hallucinogenic psilocybes belong.

How can such errors—if indeed errors they are—be explained? The growing demand for hallucinogenic mushrooms in the Huautla area has brought everybody, children and adults, many certainly much less expert than Isauro Nava, into the mushroom business. The younger generation of Indians tends to ridicule the use of mushrooms in ceremonies and is inadequately familiar with the characters of the mushrooms. Nevertheless, all these collect to fill the sudden demand at relatively high prices, and so inactive mushrooms are often mixed with active ones either by mistake or as conscious adulteration. I have witnessed the impurity and possible falsification of the product sold in Oaxaca, not easily discovered by anyone but a mycologist, especially if the material has been dried crudely for use between seasons. If substitution is discovered, the natural reaction of the seller is to claim that these different mushrooms are also used as hallucinogens.

As a result of the foregoing discussion, we may consider as established hallucinogens the following species of the Huautla region: (1) *Psilocybe cubensis* (Earle) Sing., (2) *Ps. caerulescens* Murr., and (3) *Ps. mexicana* Heim, and may add tentatively (4) *Ps. candidipes* Sing. & Smith (**17**).

By the end of July a further trip was organized by the National Autonomous University of Mexico, Institute of Biology, which took us by automobile to the region of Tenango del Valle (FIG. 1) southwest of Mexico City. A species of agaric is prescribed there by a "curandera" of a small village above Tenango and at times sold in the market at Tenango; it is currently collected by many local inhabitants of the region for storage, to have ready in case of illness, especially stomach troubles. The specimens come from a place called Piedras Blancas on the slopes of Cerro de Toluca. From our investigation on good specimens obtained at Piedras Blancas, and from observations on pure cultures made from them, we believe that they are an independent species, and not a variety of any known species, as suggested by Heim (**4**). We add therefore (5) *Ps. muliercula* Sing. & Smith (**17**), "mujercitas."

A similar trip, a week earlier, was made to San Pedro de Nexapa

near Amecameca (FIG. 1) in the Distrito Federal and at the borderline with Puebla. This trip in search of the species previously described (from purchased specimens) by Heim as *Psilocybe aztecorum* yielded no specimens, and we had to rely for the moment on material which did not produce cultures. The information about the use of the mushroom was, however, obtained from the informant in Nexapa interviewed by Heim, and the exact habitat of Heim's *Ps. aztecorum* was carefully studied. Since the fruiting bodies appear only later in the year, G. Guzmán followed this exploratory trip with a second one in September, from which good specimens were collected at their natural habitat, and cultures were taken from the lamellae of these. The use made of *Ps. aztecorum* seems to be exactly the same as that made of *Ps. muliercula*. Consequently we list (6) *Ps. aztecorum* Heim.

All six species enumerated have a number of important characters in common—first of all the diagnostic characters of the genus as defined by Singer (**16**). They are devoid of chrysocystidia, do not show a glutinous or viscid veil on the stipe, and have the stipe centrally attached. The spore print is fuscous sepia or dark purple brown (often more deep lilac when quite fresh), as is usual in the entire subfamily Strophariodeae of which *Psilocybe* is a genus. The spores are smooth and have a germ pore. Some species have rather strongly longitudinally compressed spores, although with few exceptions the compression is not strong enough to be the same as that observed in the true deconicas,[5] and the spore size is variable from species to species (4–17μ long). The upper layer of the pileus is a cutis, with a more or less individualized epicutis which often takes the appearance of a pellicle. A veil is present in all these species but the extent of development of the veil in adult specimens varies according to, and to a certain degree even within, the species. Some species have a persistent although never furrowed ("lamellar") thin repand annular veil. *Psilocybe candidipes* has an abundant veil development, but the annulus is narrow and not persistent. *Psilocybe caerulescens, Ps. aztecorum,* and some other species still have a well developed veil, but it is obliterated in age and never forms an annulus. In *Ps. mexicana,* on the other hand, is reached the extreme situation in this group, where the veil consists merely of a number of fine silky hyaline fibrils connecting the apex of the stipe with the margin of the pileus when the carpophore is young, collapsing on the stipe to form appressed scattered silky fibrils which disappear completely in age.

[5] Dr. A. H. Smith thinks that species with strongly lentiform rhombic spores of small size should not be generically separated from *Psilocybe*. It is possible, and even probable, that the study of a large number of species not yet analyzed will corroborate this opinion when the genus is finally monographed.

Aside from the generic characters indicated above, all the species that enter our list of Mexican hallucinogens have a very interesting and striking chemical character, one that is very constant in young and fresh material, but becomes lost in old and dried material, especially where the climatic conditions provide relatively high temperature. When the fruiting bodies are scratched or handled, or dried out, they stain blue or (in superposition on a yellowish pigment) green. This is apparently an enzymatic oxidation or autoxidation which may be comparable with that of *Russula* sect. *Nigricantinae* (where tyrosinase is the enzyme active in producing through the oxidation of tyrosine a melanin-like blue or pink and eventually blackening substance), or of the bluing boletes like *Boletus luridus* (with boletol, the pigment resulting being blue). The reaction is certainly identical with that observed in related genera of Agaricales like *Copelandia* and in certain species of *Pholiotina*. Some reagents such as guaiac solution accelerate this reaction in the few cases where I could make the test, but the action of guaiac is said to be nil by other authors in other cases. However, a chemical character which accompanies the bluing phenomenon is that of metol, which gives a constant strongly positive reaction with the context of the stipe in the bluing psilocybes, becoming deep purple after a few minutes (Singer **15**, **16**). Furthermore, it appears that the odor and taste of the whole group are sometimes distinctive: the odor of fresh carpophores is that of fresh flour or cucumber, or more rarely absent, or raphanaceous; while the taste is either hardly distinctive or more or less astringent or unpleasant. Heim (**5**) also indicates, among the characteristics of the hallucinogenic group, the fact that the spores show a light ocher pigmentation. It should not be denied that a very large number of Strophariaceae—Stropharioideae may show a light ocher color when seen under moderate magnifications in strong light or when not fully mature. However, my findings, corroborated by other observers, do not support the generalization that this particular light ocher color is characteristic for the Mexican hallucinogenic psilocybes or for the section of *Psilocybe* in which they belong.

Ecologically, however, all these species (even though not all the species which taxonomically belong with them) are adapted to conditions brought about by either cattle raising or agriculture, or else by natural but violent and profound disturbances of the equilibrium of the soil flora. Although not one of the species is carbonicolous or ruderal, the specific ecology of the Mexican species has apparently much in common with the ecology of anthracophilous and ruderal agarics.

With the characteristics indicated above, the hallucinogenic mushrooms enter quite naturally a taxonomic subdivision proposed by this author in 1948 (**15**) as the section *Caerulescentes* Sing., with *Psilocybe*

cubensis as the type species. This section consisted even then of one annulate and several exannulate species. The fact that both annulate and non-annulate species enter the section now, having in common, in addition to their anatomical and chemical characters, the physiological activity referred to as "hallucinatory" (in reality a complex action) or as provoking cerebral mycetisms, tends to show that the section *Caerulescentes* is a natural one, whatever weight conservative authors may still give the veil characters in other groups of agarics. The fact that *Ps. cubensis* is among the hallucinogenic mushrooms will thus serve as an additional argument in favor of its transfer from *Stropharia* to *Psilocybe* (Singer, **15**) where its real affinities are. Why, in view of the considerable evidence in favor of its transfer, Heim (**3**) retains the species in *Stropharia*, with the cryptic remark "ils [*i.e.*, *Ps. cubensis* and synonyms or related species] restent cependant apparentés avec *Stropharia squamosa* Fr. ex Pers.," [6] is not recorded.

The type of vegetation in which hallucinogenic psilocybes occur is not uniform. The vegetation found in the Huautla region (and apparently in other areas where hallucinogenic mushrooms were observed in Oaxaca) is markedly different from that in Mexico and Puebla, further north and higher up. The Oaxaca localities, or, more properly, the Huautla region, can be characterized as transitional between tropical montane and temperate montane, the tropical montane zone being immediately adjacent in the ravines below 1500 m and the temperate montane zone in the alder forests above 2000 m altitude. The tropical montane region adjoins farther down and farther east the more truly tropical rain forests, as seen in the lower-level forests of Santa Cruz—near Jalapa, for example, where Murrill collected—and the transition zone characteristic of the localities where hallucinogenic psilocybes abound may well be likened to the South American fog- or cloud-forest. It differs, however, in at least one important point: the Mexican forests are rich in trees belonging to the order Fagales, especially in evergreen oaks, which determine the mycoflora and make the presence of abundant ectotrophic mycorrhiza possible. In many places in this transitional

[6] This is a species so different from both typical *Strophariae* like *S. aeruginosa* and typical psilocybes like *Ps. semilanceata* (because of the combination of characters of the cystidia and the hypodermial and hymenophoral trama-structure) that it has been pointed out by Kühner (**7**) as anatomically closer to *Hypholoma*. For that reason it was transferred by Singer (**16**) to the genus *Naematoloma* (= *Hypholoma* sensu Kühner). *Stropharia squamosa*, or better *Naematoloma squamosum*, differs sharply from both typical stropharias and typical psilocybes in habitat requirements also, being, like so many naematolomas, a wood-inhabiting species; this ecological character of course also occurs in other genera, and in itself cannot be considered to be decisive.

zone or modified cloud forest limestone crops out, and a high percentage of calcium may be expected in soil samples, especially from our *Ps. mexicana* habitats. The rainy season extends over the entire summer, and the rains are extraordinarily abundant and almost continuous for weeks in certain times of the year.[7]

The often torrential rainfall, in combination with the quality of the soil and the steepness of the mountain sides, creates a situation quite comparable to that in the upper Yungas in South America. Here as there frequent earth and stone avalanches cover the vegetation and bring the subsoil and deeper layers to the surface. This process is particularly accelerated by the methods of agriculture and will be speeded further by roadbuilding.

The natural forest, interspersed with small pastures, fields (mostly sugar cane, some corn), and now an increasing number of coffee plantations, is partly preserved, and contains, aside from tropical and endemic elements and the species of *Quercus* already mentioned, some elements in common with the subtropical and temperate forests of the southeastern United States from North Carolina to Florida. Such elements among the trees are *Liquidambar styraciflua,* among the fungi *Hygrophoropsis tapinia* Sing., and among the species referable to *teonanácatl, Psilocybe caerulescens* Murr. At the same time one observes numerous species of *Marasmius* which prove the tropical relations of this region. All to-

[7] The climate of this transitional-vegetation area where all our Huautla material came from varies between limits such as those quoted for the two extreme localities Huauchinango (Puebla) and Jalapa (Veracruz), the one being more similar to the upper limit of the Huautla zone, the other being at the lower level of the tropical montane zone. In these two comparable localities temperature records (°F) are:

Locality	Lowest minimum	Highest maximum	Ave. coldest month	Ave. hottest month	Ann. ave.
Huauchinango	25	104	50	66	60
Jalapa	36	99	58	68	64

The observed precipitation (inches) as rain:

Locality	Ave. ann. precip.	Ave. driest month	Ave. wettest month
Hauchinango	87.4	1.9 (Febr.)	15.6 (Sept.)
Jalapa	62	1.8 (Dec.)	11.6 (June)

The data are based on Vivó and Gomez, Climatología de México, Inst. Panamer. Geol. e Historia publ. 19, México, 1946, quoted from Miranda & Sharp (**8**).

gether, the mycoflora of this transition region is just as heterogeneous as the tree flora. As one ascends, entering the *Alnus* stands at about 2000 m, just above the transition zone, one might expect to encounter a fungous flora with even more distinctly northern links. This is not the case. The mycorrhizal partner of the alder is the same as that found at the south tip of the alder area in South America, a bolete, *Gyrodon monticola* Sing., absent from the United States and Canada.

The hallucinogenic psilocybes fruit during early (spring) rains and until fall. *Ps. cubensis* seems to be one of the earliest-fruiting species; I have observed fruiting in spring in Florida. But it continues producing fruiting bodies during the entire season. The habitats of all the species in the Huautla region are characteristic. *Ps. cubensis* is dung-inhabiting. It occurs on pastures where cattle have grazed, or among sugar cane residues, but usually where the substratum has at least been mixed with cow dung. Sugar cane mulch, but without dung, is also a habitat of *Ps. caerulescens*, but it grows just as often on other plant material or around living culms of *Saccharum* on the earth of the fields. The same situation can sometimes be observed of *Ps. mexicana*. However, *Ps. caerulescens* grows mainly in shaded places in plantations or shaded fields, while *Ps. mexicana* prefers sunny open fields and pastures. *Ps. caerulescens*, according to the statements of the Mazatec Indians whom we consulted, regularly inhabits the surface of old landslides, two or more years after the landslide has occurred. We found this observation correct as far as the Huautla stations are concerned, and the description of the type locality in Alabama coincides in type of soil with that seen by us. On the other hand, the open pasture land on which *Ps. mexicana* is found is probably mostly man-made, or at least is maintained in its present condition by the grazing of animals. *Ps. candidipes* grows characteristically on the cleared surface of the earth among tree leaves fallen to the ground under *Coffea* and its shade trees (especially *Inga*). According to our Indian informants, especially Isauro Nava and his neighbors and relatives, and our own observations in this region, *Ps. candidipes* always occurs near the habitats of *Ps. caerulescens* and when found serves as an indication that *Ps. caerulescens* is not far.

The Mazateco name for *Ps. mexicana* is according to Isauro Nava a word he wrote for us and that sounded like the Spanish pronunciation of *di-nizé*, and which means a bird (diminutive), supposedly, always according to Isauro, because it makes you sing happily like a bird.[8]

[8] Mr. George M. Cowan, a student of the Mazateco language, was kind enough to offer the following comments: "We use what we choose to call a practical orthography in all published materials used by Mazatecs now. This is simply a

For *Ps. caerulescens* the indigenous name noted is *di-ki-sho* (or what sounded like this); it was explained that *di* stands again for the diminutive and *ki-sho* means landslide, this name being related to the habitat of the fungus.[9] For *Ps. cubensis* we were given two native names, one being San Isidro, which is self-pronouncing, and the other what sounds like and was transcribed as *di-shi-tjo-le-ra-ja,* which means steer mushroom in a diminutive form.[10] It is quite obvious that San Isidro stands for an earlier heathen god who was supposed to speak through the mushroom. It is also obvious that the relation of the fungus with the steer is again that of habitat, since in the Huautla region the species grows mostly on cattle dung. *Ps. candidipes* is referred to as *'nchè-jè 'nchè-jè* (Isauro's spelling).[11]

The two montane-temperate to subalpine-frigid habitats in the *pinares* (pine woods region) of the mountains nearer Mexico City mentioned above as harboring two hallucinogenic psilocybes (*Ps. aztecorum* and *Ps. muliercula*) differ from the transition forest of the Mazatec region not only climatically but likewise in the type of vegetation. The mushrooms do not, apparently, depend in any way on the

phonetic alphabet adapted as far as possible to the Standard Spanish alphabet. Tone is significant in Mazateco; the numbers $^{1\ 2\ 3\ 4}$ represent relative pitch of the syllables; ^{1} represents the highest, ^{4} the lowest level. [The symbol] (') cannot be transcribed in English orthography and is not heard by the untrained ear; it is sort of a glottal catch preceding the following sound." The correct phonetic spelling of *di-nizé* is, according to Mr. Cowan, 'nti^{1}-ni^{4}-se^{3}; it is pronounced ndee^{1} nee^{4} say^{3}; nti = ndee means an affectionately regarded object (referring to the mushroom) and ni-se, bird.

[9] Mr. Cowan's comments indicate that here as in the case of *Ps. mexicana* Isauro's names are current abbreviated words, omitting between the *'nti* and the *ki-sho,* the general term for mushrooms, *xi*^{3}*-tjo*^{3} ("which comes out," presumably of the earth), so that the full name of *Ps. mexicana* would be *'nti*^{3}*-xi*^{3}*-tjo*^{3}*-ni*^{3}*-se*^{3}, and for *Ps. caerulescens: 'nti*^{3}*-xi*^{3}*-tjo*^{3}*-qui*^{3}*-xo*^{1}, pronounced *ndee*^{1}*-shree*^{3}*-t(h)oe*^{3}*-kee*^{3}*-shro*^{1}, meaning dear little thing that comes out of the earth of a landslide. The *x* is a sound as if English sh and r were pronounced at the same time; j and qu are pronounced as in Spanish, *i.e.* as a more aspirated *h* and a *k* respectively. "Tsami kishu" given by J. B. Johnson (quoted from Schultes, **13**) evidently refers to this same species.

[10] G. M. Cowan spells this *'nti*^{3}*-xi*^{3}*-tjo*^{3}*-le*^{4}*-nčha*^{4}*-ja*^{4}, pronounced *ndee*^{1}*-shree*^{3}*-t(h)oe*^{3}*-lay*^{4}*-njra*^{4}*-ha*^{4} (meaning as above: the dear little thing that comes out pertaining to the steer or ox). The pronunciation of čh is described as a sound similar to English *j* (in judge) and *r* (in run) if pronounced simultaneously.

[11] Mr. Cowan, who had a special interview about this new species with Isauro and friends, explains that this means, as Isauro had already told us, "a signal of," in reference to the other hallucinogenic mushrooms, particularly *Ps. caerulescens,* which will appear here or nearby later. The correct spelling is *nche*^{4} *je*^{4}, pronounced in English like njre^{4}-he^{4}.

detritus or the presence of living roots of the characteristic pines (*Pinus hartwegii* with *Psilocybe aztecorum*, *Pinus pseudostrobus* with *Ps. muliercula*). Neither do they live on agricultural land or dung, but directly on the earth, naked earth on the banks of mountain streams with occasional salt outcroppings, following the ravines around 3000 m elevation, or else (*Ps. aztecorum*) among grasses and (rosaceous) herbs in openings, often on the slopes of steep ravines even higher up (between 3300 and 3700 m altitude). The subalpine pine woods are here beginning to thin out and approach the absolute timber line (at about 4000 m). The psilocybes are accompanied by those mycorrhizal Basidiomycetes which make the survival of these pines possible at such an altitude, especially *Amanita inaurata* Secr., various species of *Lactarius*, and *Suillus* aff. *brevipes* (Peck) Sing. Non-mycorrhizal Basidiomycetes of this vegetation are *Phlogiotis helvelloides* (Fr.) Martin, *Tubaria* sp. (on *Pentstemon barbatus*), and *Laccaria* aff. *laccata* (Scop. ex Fr.) Berk. & Br. Among the Ascomycetes are *Cordyceps capitata* (Fr.) Link (on *Elaphomyces*) and *Hypomyces lactifluorum* (on *Russula delica*), the former often collected as a remedy for various diseases but doubtfully hallucinogenic,[12] the latter sold in the food markets. In the Piedras Blancas region on Cerro Toluca the presence of *Amanita calyptratoides* Atk., a western North American species, is remarkable; the southeastern race of *A. muscaria*, also a hallucinogenic mushroom of a sort, and almost constantly accompanying pine mycorrhiza, is common in the neighborhood of the psilocybes, but has never been mentioned as a locally accepted drug.

While the substratum of both *Ps. aztecorum* and *Ps. muliercula* is apparently comparable to that of *Ps. caerulescens* (more or less unstable or shifting bare soil), the climatic conditions and the surrounding vegetation are very different in this region from the *Psilocybe* habitats in Oaxaca. There is frequent freezing in the altitudes indicated, and the precipitation is not so abundant here as in the Mazatec country. During the summer-fall rainy season, precipitation is heavy enough to maintain a relatively rich flora of large fleshy Basidiomycetes reminiscent of that further north in Mexico and in the United States. This, obviously, is possible only because of the relatively lower temperatures, even in summer, whereby evaporation is kept at a minimum.

[12] It is remarkable that another species of the same family, *Cordyceps sinensis*, growing on insects, is widely used as a medicine in China, while still another species of the Hypocreaceae, *Claviceps purpurea*, ergot, is the source of several alkaloids which have only recently been studied thoroughly. In view of this, it is very probable that the Mexican medicinal hypocreaceous species would be well worth a special investigation, particularly from the biochemical point of view.

Psilocybe aztecorum is known as *niños del agua* (Spanish: children of the water; this is apparently an allusion to their habitat along the ravines). *Ps. muliercula* from Piedras Blancas is also known as "niños," but as such it is only one of the elements referred to by the more general term niños which includes "mujercitas" and "hombrecitos" (little women and little men). Only the "mujercitas" are agarics (*Ps. muliercula*); the "hombrecitos" are *Cordyceps capitata* (Fr.) Link (det. Mains). There is an obvious misinterpretation of these names in the literature. Although "mujercitas" are correctly interpreted as *Psilocybe*, the term has been thought to refer to a variety of *Ps. mexicana*. Dr. Herrera and the author, however, found the difference in external appearance and habitat constant enough to separate the "mujercitas" from *Ps. mexicana*, inasmuch as in all natural habitats of the two species the spore size is consistently different. On the other hand, "hombrecitos" have been interpreted as merely smaller individuals of *Ps. mexicana* var., or, since hallucinatory mushrooms in Mexico are always given in pairs, the complementary individuals—in other words, part of the same drug. Our own interpretation has been reconfirmed several times, and it is also obviously the logical interpretation, since the allusion to the shape of the respective fruiting bodies is self-explanatory, and the terms lose all descriptive significance if Heim's and Wasson's explanations are accepted.

It is interesting to note that not only are the conditions under which the respective fungi develop widely different, but the use made of the mushrooms is likewise different, in the main hallucinogen-producing states of Mexico visited by me. The Nahua Indians, according to the data obtained by us in discussions with inhabitants of San Pedro de Nexapa and Tenango del Valle as well as the mountains near these villages, do not talk about the hallucinogenic effect of the mushrooms, but volunteer information merely on their healing qualities. In these villages, the use is strictly a matter of religious healing, the business of the curandero or curandera. Permission has to be granted by God in the curandero's dream before the drug can be employed safely. On the other hand, the Mazatecs talk freely about the hallucinogenic and euphoric effects of these mushrooms, and eat them for precisely that effect. The religious healing ceremonies of the Mazatecs are also directed by curanderos, but more emphasis is given to the revelations obtained by the intoxicated persons, so that the use made of the mushroom in Huautla is at least partly divinatory rather than directly medical. Whether this corresponds to any difference in the chemicals present in the respective species, or merely to ethnological factors, cannot

be stated at present. At any rate, the Mazatecs seem to have preserved more of the original Aztec lore about *teonanácatl* than the people living now in Aztec country, who are at least in part the direct descendants of the Aztecs. It is of course possible that the secretive and exclusive use the Nahuas make of their "niños" is a result of more complete repression and conversion in the early times of the Spanish rule, when the Oaxaca Indians of the Sierras were practically left to their own devices.

From all the species mentioned above, including also *Panaeolus sphinctrinus*, both tissue cultures and spore germinations were obtained.

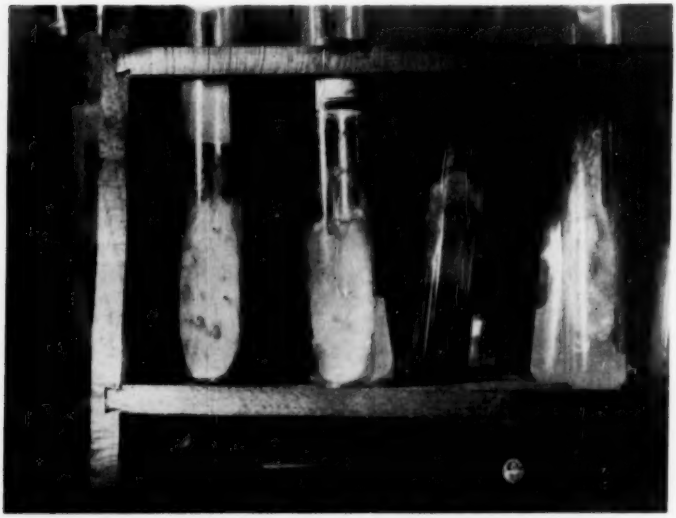

FIG. 2. *Psilocybe cubensis*. Stringy mycelium (upper portion of slant in tube at extreme left) and primordia. Phot. R. Singer.

The tissue fragments grew well at the room temperatures of Mexico City in July, some even better at 27–29° C, and better on malt-extract agar and Kauffman's (modified) medium than on potato-dextrose agar. These were the first pure cultures obtained directly from fruiting bodies at their classical habitats. Subcultures have been deposited at the Instituto Politécnico and the Instituto de Biología of the University of Mexico, at the Department of Botany of the University of Michigan, The New York Botanical Garden, and the Phytopathology Laboratory of the Ministerio de Agricultura y Ganadería in Buenos Aires, all in

personal care of responsible scientists for specified further research on these organisms. For the sake of comparison, isolations were also made from North American spore prints of *Psilocybe caerulipes* (Peck) Sacc. (northern Michigan), also belonging to the section *Caerulescentes*, and from *Copelandia caerulescens* (Berk & Br.) Sing.

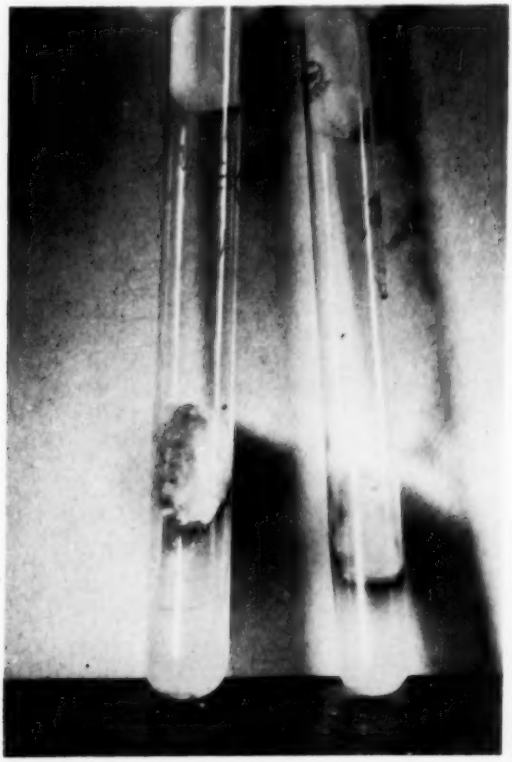

FIG. 3. *Psilocybe mexicana*, showing the dark discoloration of the medium beneath the whitish mycelium in both test tubes. Phot. R. Singer.

Panaeolus sphinctrinus, *Psilocybe cubensis*, *Ps. caerulescens*, *Ps. candidipes*, and *Ps. mexicana* were checked by Dr. W. J. Robbins for antibiotic activity. None was evidenced against *Staphylococcus aureus* or *Escherichia coli*, and the action against *Mycobacterium smegma* was slight.

Psilocybe cubensis has been observed to form a stringy mycelium in malt-agar test tubes. Mycelium of this species, more than that of other species studied in pure culture, has a tendency, greater at lower temperatures than at higher ones, to turn blue in culture. *Ps. cubensis* also tends to produce most easily what might be termed white rhizo-

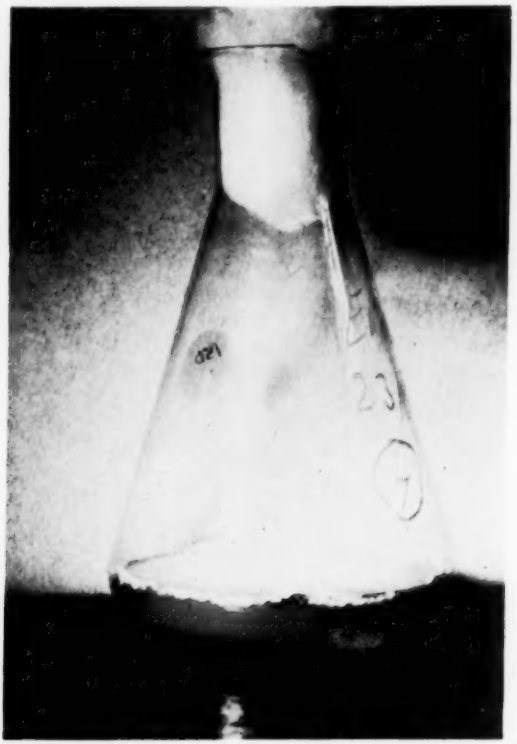

FIG. 4. *Psilocybe caerulescens.* Typical mycelium culture in Erlenmeyer flask. Phot. R. Singer.

morphs in the stringy portions of the mycelium, and a large number of small fruiting bodies on the agar (FIG. 2). These carpophores or primordia do not always attain full size during later development, and often fail to mature; they tend to turn blue without being handled. The agar cultures of *Ps. mexicana* have a tendency to turn deep brown in contact with the mycelium (FIG. 3). On partially drying out they also

FIG. 5. *Panaeolus sphinctrinus*. Abundant carpophore production in artificial mushroom house culture, natural size. Photog. Serv. Penn. State Univ., courtesy Dr. L. R. Kneebone.

frequently produce normal fruiting bodies. On the other hand, *Ps. caerulescens* under the conditions in which it was kept in the laboratory did not form white rhizomorphs or fruiting bodies in pure culture, and the mycelium merely colors the medium light brown (FIG. 4). In Czapek with 1% sucrose and vitamins, *Ps. caerulescens* produced aerial mycelium which broke down into "oidia" (mycelial fragments often referred to as arthrospores), observed for the first time by Dr. R. Ames. The mycelium of the *Panaeolus* remains pure white and fluffy without distinct discolorations, rhizomorphs, or fructifications. The same is true for other psilocybes except *Ps. muliercula*, which tends to form a slightly brownish aerial mycelium.

Panaeolus sphinctrinus (FIG. 5) and other species of *Panaeolus* grow in mushroom-house conditions as well as or better than *Agaricus bisporus* (Lange) Sing., the cultivated mushroom. The psilocybes were also grown not only under laboratory conditions in large glass containers (FIG. 6), where some produce large fleshy fructifications, but also in greenhouse conditions (FIG. 6) on compost trays, where the method used by commercial mushroom growers had to be considerably modified.

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This cooperation continued in the United States. Dr. K. L. Jones, Head of the Department of Botany, University of Michigan, and Dr. E. B. Mains, Director of the University Herbarium, made it possible

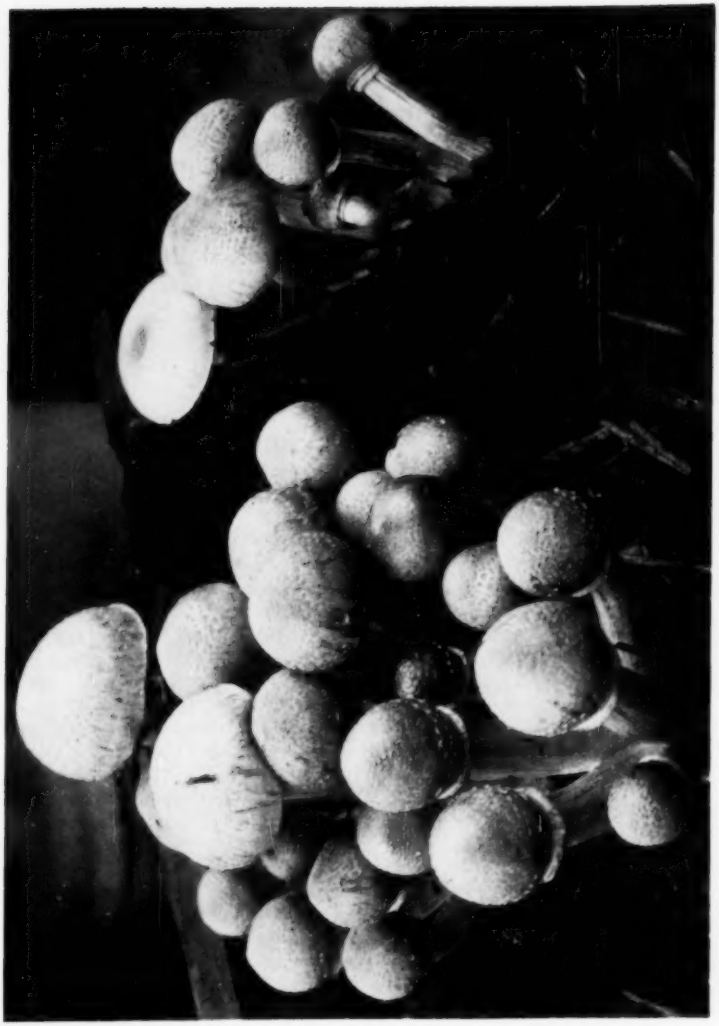

FIG. 6. *Psilocybe cubensis*. Greenhouse culture on uncased tray with compost, slightly reduced. Photog. Serv. Penn. State Univ., courtesy Dr. L. R. Kneebone.

for me to carry out part of the research in Ann Arbor. Dr. A. S. Sussman was particularly kind in supplying the necessary equipment and in providing valuable advice to me and my collaborators in the Department of Botany. He as well as Dr. A. H. Smith offered interest and encouragement.

It should also be stated that had it not been for the consistent initiative and the financial backing of the Bertram and Roberta Stein Neuropsychiatric Research Program, Inc., of Chicago, the present work would not have been possible, and the investigations now in progress elsewhere would have had no chance of realization. I am particularly indebted to Dr. Sam I. Stein, Executive Medical Director of the organization.

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MYCOLOGICAL INVESTIGATIONS ON TEONANÁCATL, THE MEXICAN HALLUCINOGENIC MUSHROOM.[1]

PART II. A TAXONOMIC MONOGRAPH OF PSILOCYBE, SECTION CAERULESCENTES

ROLF SINGER AND ALEXANDER H. SMITH

(WITH 50 FIGURES)

As has been shown by Rolf Singer in Part I of these studies, it may be accepted as probable that the majority of the hallucinogenic mushrooms of Mexico belong to the section *Caerulescentes* of the genus *Psilocybe*. It is not yet known whether all species of the section possess hallucinatory properties, but it is probable that all or at least many of them are hallucinogenic or poisonous, causing cerebral mycetism with or without other symptoms. At all events, a critical taxonomic account of the species in this section is highly desirable to facilitate a biochemical survey of the group. This contribution is a part of two major projects, first the research on hallucinogenic mushrooms carried out by the Bertram and Roberta Stein Neuropsychiatric Research Program Inc., Chicago, Illinois, and second, a monograph of the North American species of *Psilocybe* now in preparation by A. H. Smith.

We wish to express our thanks to the curators of the following institutions from which we have received material for study: Kew Herbarium (K), Dr. G. Taylor, Director, and Dr. R. W. G. Dennis, curator; Farlow Herbarium (FH), Dr. I. M. Lamb; New York Botanical Garden (NY), Dr. D. P. Rogers. Our own collections and those obtained from correspondents are on deposit at the Instituto Miguel Lillo (LIL), Tucumán, Argentina, and at the Herbarium of the University of Michigan (MICH). Valuable data were obtained for us by G. Guzmán, Mexico D.F.

The color terms used in the descriptions were taken from R. Ridgway, Color Standards and Color Nomenclature, Washington, D.C., 1912, and Maerz and Paul, A Dictionary of Color, 1st edition, McGraw-

[1] Papers from the University of Michigan Herbarium and Department of Botany no. 1074, University of Michigan, Ann Arbor, Mich.

Hill, New York, 1935. Those from Ridgway are within quotation marks and those from Maerz and Paul are underlined.

In giving the measurements of spores the length is given first and the width second, but if the spore is somewhat compressed and broader than deep, the width is given following the length and the depth (i.e. breadth in side view or profile) is given last—for example, 8–11 × 6–7 × 5–6 μ. Measurements of the cystidia (including cheilocystidia) give the length first, the width of the broadest part next (usually the diameter of the basal or central enlargement), then follows the diameter of the "neck" (thinned apical portion) or the narrowed part above the mid-portion, unless the apex is described separately.

The cultural characters as far as now available are not part of the descriptions provided in this monograph since the cultures were described by Singer in Part I. Nevertheless, some of the data provide interesting and even diagnostic characteristics of certain species.

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PSILOCYBE sect. CAERULESCENTES Sing., Sydowia **2**: 37. 1948.

Pileus white or pigmented, slightly lubricous to almost glutinous in wet weather, pellicle often separable; lamellae ascending or horizontal, usually adnate, in some species subdecurrent, in others sinuate-adnexed, edges pallid, faces pallid to brownish, becoming purple brown from the spores; stipe slender to fairly robust, strongly purple with metol (p-metylaminophenol-sulfate), usually bluing with guaiac solution, typically bluing when wounded or blue color becoming evident on surfaces or mycelium under certain conditions of growth or in age or on drying.

Spores purple fuscous to lilac in fresh deposits or in water-mounts under the microscope, *after dehydration and then mounting in KOH* becoming dark yellowish brown, terete to laterally compressed and variable in shape from species to species, smooth, wall complex, apical pore distinct and typically causing the apex to appear truncate; basidia typically 4-spored, pleurocystidia present or absent but if present not as chrysocystidia (species with chrysocystidia excluded from *Psilocybe* by definition); cheilocystidia abundant and often causing the gill edge to be heteromorphous (completely sterile and sterile elements different from those of gill face), or nearly so; subhymenium and hymenopodium well developed, gill trama either regular or showing a mediostratum and lateral strata (between the mediostratum and the hymenopodia on each side); cuticle of pileus consisting of a gelatinous or subgelatinous pellicle

or an almost non-gelatinous epicutis (upper layer) and a well-differentiated hypodermium (lower layer), the epicutis (pellicle) of narrow more or less hyaline hyphae, the hypodermium a more compact layer consisting mostly of enlarged hyphal cells but some narrow filaments also present; clamp connections consistently observed on hyphae of all types and at the base of the basidia of the species described below.

SUMMARY OF THE STIRPES

Stirps. CUBENSIS

Spores medium to large (7.7 μ or more long) and mostly somewhat compressed, in face view obscurely to distinctly angular-ovate to angular-elliptic; veil typically membranous and the remains persisting on the stipe as a membranous annulus; aspect of carpophores not mycenoid; habitat on dung or rotten wood.

The combination of veil and spore characters is diagnostic of the stirps. The presence of a membranous annulus would cause these species to be classified in *Stropharia* in classical taxonomic arrangements, but the lack of chrysocystidia and the presence of a change to blue when injured point to close relationship with the other species of the section. The true *Strophariae* have chrysocystidia or a viscid to glutinous universal veil. Other species such as *P. aztecorum* and *P. candidipes* may at times show a narrow annulus but these have terete or only very slightly compressed spores.

Species included: 1. *P. cubensis,* 2. *P. subaeruginascens,* and 3. *P. aerugineomaculans.*

Stirps. YUNGENSIS

Spores very small (less than 7.7 μ long) and strongly compressed, typically angular-ovate in face view; veil floccose over the lower part of the stipe but not forming an annulus; pileus relatively high or acutely papillate; stipe thin; cap margin incurved at first (general aspect almost mycenoid but with incurved margin); habitat on forest litter and much decayed wood particles in the tropical zone; pigmentation dark, hyphae of the hypodermium heavily incrusted.

The combination of floccose veil and the uniquely small and compressed spores along with the characteristic habit determine the stirps which, so far, contains only a single species.

This stirps has as much in common with the deconicas as the preceding has with the stropharias. It differs, however, in habit and chemical

characters from the species usually classified in *Deconica*. Within the section it seems to come closest to the two smaller-spored representatives of the preceding stirps, which are also characterized by relatively small carpophores.

Species included: 4. *P. yungensis*.

Stirps. MEXICANA

Spores compressed, medium sized (7–11 μ long); veil thin and poorly developed, not leaving traces on mature carpophores; pileus acute or obtuse in outline except for an apical conic papilla, with straight margin when young, or margin bent in slightly; pellicle poorly developed; stipe thin; habitat characteristically in pastures, fields, meadows, or generally outside the forest in tropical-montane vegetation or plantations.

This stirps forms a natural transition between the preceding and the following one. The spores are still compressed but are not characteristically small; the habit is mycenoid though perhaps slightly less so than in stirps *Silvatica*.

Species included: 5. *P. mexicana*

Stirps. SILVATICA

Spores not compressed, medium (6–9) to large (10–13 μ long); veil thin and not leaving traces in adult carpophores; pileus relatively high and acute, not fully expanding, with straight margin, thus habit mycenoid; pellicle present, thin to thick; habitat in forests on wood and debris, but extratropical (as far as known).

Species included: 6. *P. silvatica*; 7. *P. pelliculosa*.

Stirps. CYANESCENS

Spores varying from slightly compressed to terete, typically 9 μ or more long; veil varying from well developed (in *P. aztecorum*) to poorly developed, but never floccose or annulate; habit typically collybioid or nearly so; habitat terricolous or on rotten wood in forests, parks, or among scattered trees.

This combines all the large-spored exannulate species which do not have a mycenoid habit. The spores are not even obscurely angular in face view and are terete or at best only slightly compressed. It is remarkable that the habitat is rather similar in all of them and that none of them can be described as truly tropical.

Species included: 8. *P. aztecorum*; 9. *P. cyanescens*; 10. *P. collybioides*; 11. *P. strictipes*; 12. *P. bacocystis*.

Stirps. CAERULESCENS

Spores compressed to terete, small (less than 9 μ long); stipe typically thick (more than 3 mm at apex); veil well developed; habit collybioid to tricholomatoid but not mycenoid; habitat variable.

The species grouped here have well developed veils and rather thick stipe; they are thermophilous in the sense that they all occur in warm climates.

Species included: 13. *P. caerulescens;* 14. *P. aggericola;* 15. *P. candidipes.*

A fourth species which might belong here, *P. zapotecorum* Heim, has not been studied by us. We prefer not to place it formally in one of the stirpes introduced here inasmuch as it might conceivably be closer to some other stirps, or represent a stirps of its own.

Supplement to stirps VI: 16. *P. zapotecorum.*

Stirps. CAERULIPES

Spores 7–9(–10) μ long, terete, stipe thin (1–3 mm at apex); veil thin and cortinate; habit collybioid; habitat on rotten wood and debris in the forest and under scattered trees.

But for the small spores and thin stipe this stirps could be united with stirps *Cyanescens.* According to spore size it would be close to stirps *Caerulescens.* But both species are either temperate or montane, and extratropical.

Species included: 17. *P. muliercula;* 18. *P. caerulipes.*

KEY TO SPECIES OF SECTION CAERLESCENTES

1. Annulus typically membranous and persistent 2
   2. Spores 11.5–17.3 μ long ..... 1. *P. cubensis*
   2. Spores smaller 3
      3. Growing on wood; pileus viscid ..... 3. *P. aerugineomaculans*
      3. Growing on dung; pileus merely moist ..... 2. *P. subaeruginascens*
1. Annulus if present merely a zone of fibrils, or very fugacious 4
   4. Spores 5–6.5 × 4.3–5 × 3.6–4 μ, strongly compressed; pileus acute ..... 4. *P. yungensis*
   4. Spores larger and only somewhat compressed or terete 5
      5. Pileus margin straight when young or almost so; habit more or less mycenoid 6
         6. Spores compressed (broader in face than in side view); growing in open areas (meadows, fields) ..... 5. *P. mexicana*
         6. Spores terete; growing in woods on litter and rotten wood 7
            7. Spores 6–9.5 (–11.5) × 4.5–5 μ; pellicle thin ..... 6. *P. silvatica*
            7. Spores 9.3–11 × 5–5.5 μ (10.5–13 × 5.5–7 μ); pellicle thick and separable ..... 7. *P. pelliculosa*

5. Pileus margin incurved when young; habit typically collybioid 8
8. Spores typically less than 9 μ long 9
9. Stipe 10–20 mm thick, 100–200 mm long, cortex very fibrous, hard and elastic .....16. *P. zapotecorum*
9. Stipe not as above 10
10. Stipe white, basal half scabrous-strigose, upper half strongly floccose from veil .....15. *P. candidipes*
10. Not as above 11
11. Veil copious and flocculose in young specimens 12
12. Spores in face view 5–6 μ broad; stipe whitish when young .....13. *P. caerulescens*
12. Spores in face view 4–5 μ broad; stipe colored when young .....14. *P. aggericola*
11. Veil thin, cortinate, fugacious 13
13. Pileus not viscid .....17. *P. muliercula*
13. Pileus viscid .....18. *P. caerulipes*
8. Spores typically more than 9 μ long 14
14. Lamellae pallid to white, or brownish only at maturity—sterile to partly sterile collections of *P. collybioides* key out here
14. Not as above.
15. Stipe whitish; pileus milk white or disc merely ochraceous ....8. *P. aztecorum*
15. Stipe or pileus or both more deeply colored 16
16. Pileus chestnut color; spores slightly compressed .....9. *P. cyanescens*
16. Not as above.....17
17. Cheilocystidia 20–30 (–36) × 4–6 × 1.2–1.5 μ .....12. *P. baeocystis*
17. Cheilocystidia larger 18
18. Odor distinctive—variable, farinaceous to raphanaceous to spermatic..... .....10. *P. collybioides*
18. Odor none; taste mild 19
19. Stipe 100–130 mm long, straight..... .....11. *P. strictipes*
19. Stipe up to 70 mm long. *H. cyanescens* sensu Malençon (see under *P. collybioides*)

STIRPS CUBENSIS

1. PSILOCYBE CUBENSIS (Earle) Sing., Sydowia **2**: 37. 1948. (FIG. 1–3, 40–41.)

Stropharia cubensis Earle, Est. Agron. Cuba **1**: 240. 1906.
Naematoloma caerulescens Pat., Bull. Soc. Mycol. Fr. **23**: 78. 1907.

Hypholoma caerulescens (Pat.) Sacc. & Trott. in Sacc., Syll. Fung. **21**: 212. 1912.

Stropharia caerulescens (Pat.) Sing., Ann. Mycol. **34**: 340. 1936.

Stropharia cyanescens Murr., Mycologia **33**: 279. 1941.

Pileus 16–80 mm. broad, conic campanulate with an acute papilla at first, gradually becoming convex to plane and at times with a depression around the umbo, umbo becoming more obtuse, more rarely without any umbo or papilla, viscid, glabrous or with fugacious veil remnants near margin, white with more or less fulvous center, eventually entirely fulvous brown, sometimes white to pale yellow ("cartridge buff") at margin, more "cream buff," "chamois," or "honey yellow" toward the "Isabella color" to "clay color" disc, usually staining bluish in age or when injured.

Lamellae gray, becoming deep violet gray and somewhat mottled, finally almost black, adnate to adnexed, seceding, close, narrow, becoming ventricose in mid-portion, broad in age, edges white.

Stipe 40–150 × 4–14 mm, tubular, usually somewhat thickened downward, more rarely subequal, or tapering to the base, white, staining blue ("deep Medici blue") when injured, eventually discoloring to yellow brown or reddish cinereous, often strongly sulcate at the apex, smooth otherwise, glabrous to slightly fibrillose, dry; annulus membranous but thin, smooth on both sides, white, staining blue, fragile, usually persistent.

Context white, staining blue on injury; odor none; taste farinaceous.

Spores 11.5–17.3 × 8–11.5 × 7–9 μ, dark yellow brown (in KOH) to dark olive brown (in NH_4OH), smooth, nearly elliptic in side view, ovate to broadly elliptic in face view and many obscurely angular, wall thick and complex, apex truncate from a distinct apical pore; basidia (2-, 3-, or) 4-spored, 28–35 × 10–13 μ; pleurocystidia scattered, 18–23 × 10–13 μ, ventricose and narrowed slightly near apex to an obtuse to rounded tip, thin-walled, contents (in KOH) homogeneous (not protoplasmatic); cheilocystidia numerous, 18–35 × 6–12 μ, fusoid-ventricose with obtuse to subcapitate apex, neck 4–18 μ long, 3–6.5 μ thick, enlarged tip (head) 4–5 μ, wall thin and readily collapsing; gill trama regular, mediostratum of hyaline parallel to somewhat interwoven hyphae, in well pigmented caps this layer flanked on both sides by parallel hyphae with dingy ochraceous walls (in KOH); pellicle of pileus a thin layer of narrow (c. 3.5 μ) gelatinous hyphae which are radially arranged and yellowish to hyaline in KOH; hypodermium of interwoven to more or less radial hyphae up to 26 μ in diameter, with ochraceous brown walls in KOH; clamp connections present.

Chemical characters: metol strongly positive on context of stipe ("dark naphthaline violet" or darker), other reagents negative or accelerating the bluing.

Gregarious on cow dung, more rarely on horse dung or on rich pasture soil, or on sugar cane mulch or straw or sawdust mixed with dung, usually outside the forests, fruiting from February until November or December, south of the Equator from November until April.

Material studied: U.S.A., Florida: TYPE of *Stropharia cyanescens* Murr. and additional collections by *G. F. Weber, J. R. Watson,* and *W. A. Murrill,* as *S. cyanescens,* F-19138, F-19630, F-19244, F-17932, F-17735, F-19464 (all FLAS), and *R. Singer F 1802, F 1802a* (FH, F); Magnesia Springs, *W. A. Murrill* (NY). Puerto Rico: Mayaguez and Ailonato, *Bruce Fink 899* and *1955* (NY). Cuba: Santiago de las Vegas, *Earle 109* both on sheets and in box, marked "tipico," TYPE of *Stropharia cubensis* (NY); also *Earle 169, 315, 350;* Candelaria, *Earle 206* (NY); Soledad, Cienfuegos, *W. L. White 808, 526* (FH). Mexico: Oaxaca, Huautla de Jiménez, *7–27–38, R. E. Schultes,* Plantae Utiles Mexicanae 349 (FH); *R. Gordon Wasson 1* (NY); *R. Singer M 1512* (MICH). Brit. Honduras: *M. E. Peck 478* (NY). Trinidad (collector not given) (NY). Bolivia: Beni, Guayaramerin, *R. Singer B* (LIL). Argentina: Tucumán, *R. Singer T* (LIL). Indochina: TYPE of *N. caerulescens* Pat. (FH).

The collections enumerated above should be divided into three color varieties:

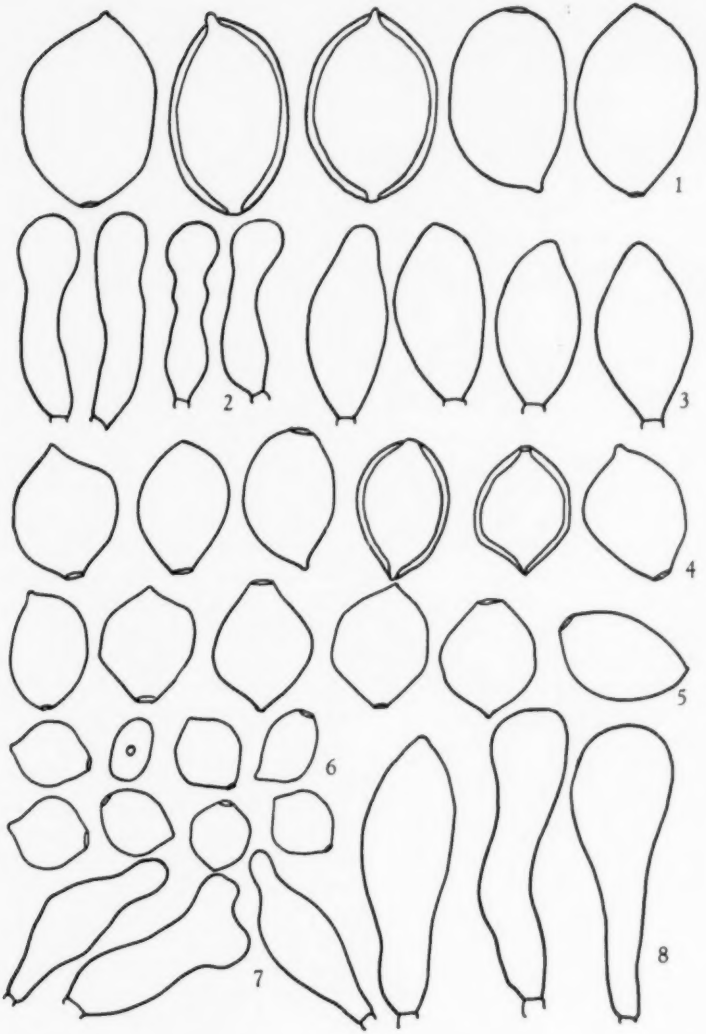
P. CUBENSIS var. CUBENSIS (the type). Here, the pigmentation of the pileus is fulvous. It develops early, and pallid pilei are hardly ever seen. The strain proved to be hallucinogenic belongs here.

P. CUBENSIS var. **cyanescens** (Murr.) comb. nov. The type of this variety is the type of *Stropharia cyanescens* Murr. It differs from the type variety in the virtual lack of pigment or its small quantity; consequently the pileus is pallid to pale isobelline. Known to occur in Florida (**10**).

P. CUBENSIS var. **caerulescens** (Pat.) comb. nov. The type of the variety is *Naematoloma caerulescens* Pat., type. It differs from the type variety in showing a clear yellow color at least in certain portions of the pileus. Known to occur in Indochina (**11**).

Illustrations: V. P. & R. G. Wasson, Mushrooms Russia and History **2**: *pl. 40, fig. 2.* 1957; Life, May 13, 1957, p. [107] *fig. at lower right.* (Both the *var. cubensis.*)

The senior author at one time (**14**) thought that *Stropharia caerulescens* Imai (*S. venenata* Imai) was identical with *S. cubensis,* but we are treating it now as synonymous with a closely related but distinct species. For more detailed commentary on *S. venenata* see under *P. subaeruginascens.*



FIGS. 1–8. 1–3: spores, cheilocystidia and pleurocystidia of *Psilocybe cubensis*. 4: spores of *P. subaeruginascens*. 5: spores of *P. aeruginomaculans*. 6–8: spores, cheilocystidia and pleurocystidia of *P. yungensis*.

2. PSILOCYBE SUBAERUGINASCENS Höhnel, Sitzungsber. K. Akad. Wiss. Wien **123**(1): 78. 1914. (Fig. 4.)

Stropharia caerulescens Imai, Trans. Sapp. Nat. Hist. Soc. **12**: 148. 1932.

Stropharia venenata Imai, Journ. Fac. Agr. Hokk. Imp. Univ. **43**(2): 270. 1938.

Pileus 15–25 mm broad, plano-convex, almost membranaceous, glabrous and smooth, whitish with smoke brown center, becoming slightly greenish-blue-spotted when touched.

Lamellae grayish brownish, rather distant, with paler edge, 2–3 mm broad, broadly adnate and somewhat decurrent.

Stipe 30–40 × 1.5–3 mm, cylindric, slightly thickened at base, somewhat flocculose-farinaceous above, otherwise glabrous, somewhat shining, hollow but stuffed with a loose woolly pith, white, weakly greenish blue when touched, with an annulus above the center of the stipe, annulus small, often oblique, scaly-membranous; mycelium abundant, filamentous, white, staining greenish blue or almost steel blue.

Context white, tough in the stipe, bluing; odor and taste not recorded.

Spore deposit beautifully violet-brownish.

Spores 7.7–10 (–11.5) × 7–7.8 × 6–7 μ, ovoid to subrhomboid in face view, in side view somewhat inequilateral, smooth, dingy yellow brown in KOH, apex truncate from a broad flattened germ pore; basidia 2- and 4-spored, very rarely 1-spored or 3-spored, 18–28 × 6.3–9.2 μ, typically with a median constriction; pleurocystidia 25–33 × 9–12 μ, broadly fusoid-ventricose with obtuse apex, hyaline, thin-walled, contents homogeneous; near the edge sometimes some pleurocystidia similar to cheilocystidia; cheilocystidia 20–33 × 6–9 μ, fusoid-ventricose with obtuse apex or neck narrow and cylindric, or in some the apex subcapitate, hyaline, causing the edge to appear heteromorphous; epicutis of pileus not gelatinous, apparently of closely interwoven appressed hyphae; clamp connections present.

Subcespitose on horse dung, Buitenzorg, Java, Indonesia, *v. Höhnel*, TYPE (FH).

This is a *Psilocybe* of the *P. coprophila* type but staining blue. The spores are more angular in face view than those of *P. coprophila* and also of smaller size.

Stropharia caerulescens Imai (**5**) is placed in synonymy here although the type is unavailable at present; we base our judgment on the following original description:

Pileus 15–60 mm broad, glabrous, hygrophanous, or scarcely slightly viscid, convex to plane to subumbonate, yellowish to isabelline, more rarely whitish, margin always pallid. Lamellae pallid, then violet fuscous, adnate. Stipe 35–90 × 5–9 mm, equal, dry, almost hollow, fibrillose below the annulus, whitish, annulus almost apical, very thin membranous, more rarely fibrillose, often evanescent. Context whitish or pallid, bluing. Spores fuscous or violet fuscous, ellipsoid, 7–10.5 × 4.25–7 μ; cystidia none. Gregarious or cespitose on earth and dung, fruiting in June, July and October. Japan, Hokkaido, Ishikari province, near Asahigawa and Sapporo. [Specimens are apparently preserved at Sapporo.]

It is interesting to read in Imai's account (**5**) about the physiological activity of this species. It caused ten deaths in 1929 alone, and is apparently more toxic than the related Mexican species. The symptoms are described as feeling feverish, with a subjective impression as if strong liquor had been imbibed; the limbs became somewhat paralyzed. In the hospital after an emetic had been administered and the stomach washed and eventually a laxative had been given, the patient was now in bed with intermittent constriction or trembling of muscles and finally there were hallucinations, then coma. This patient, a woman, recovered. Her son who did not eat the flesh of the mushroom but drank only the liquid of the soup in which it was cooked felt only paralysis of the limbs and a chill, followed by hallucination. All recovered eventually.

In another case, after similar symptoms were observed, coma, loss of consciousness, and talking in delirium were observed. The pupils had opened to a medium size and did not react to light. (This observation coincides with observations made in Mexico with psilocybes of this section.) For more details see Imai's paper (**5**).

In a later paper (**6**), Imai renamed his species *S. venenata* Imai. The description was now slightly changed to accommodate also specimens with deeper color of the pileus, more viscid surface, and habitat on rotten wood. The conclusion is very suggestive that the forms later added to the species concept and expressed in the changes of the description at the time of the publication of *S. venenata* can be accounted for if it is assumed that the type form (= *P. subaeruginascens*) was later confused with *P. aerugineomaculans*. Whether this opinion is correct can be proved only if and when specimens from Japan become available.

The original description of *S. caerulescens* Imai is accompanied (p. 149) by a photograph which, by implication, and with certain reservations, may be cited as an illustration of *P. subaeruginascens* Höhnel.

3. **Psilocybe aerugineomaculans** (Höhnel) comb. nov. (FIG. 5.)

Stropharia aerugineomaculans Höhnel, Sitzungsber. K. Akad. Wiss. Wien **123**(1): 78. 1914.

Pileus 25–40 mm broad, campanulate, becoming expanded and umbonate, surface slightly viscid to the touch, disc dark blue, remainder reddish gray-cinereous (as in *Psathyrella gracilis* sensu Höhnel), margin striatulate.

Lamellae rather distant, 4–5 mm broad—*i.e.*, moderately broad—attenuate-adnate, yellowish olive, marbled as in *Panaeolus*, edges even.

Stipe 40–50 × 2 mm, not thickened at base, cylindric, hollow, white, slightly flocculose, glabrescent, shining, annulus membranous, small, entire, white; rind 0.15 mm thick when dried.

Context in the middle of the pileus thin (2 mm), membranous toward margin, somewhat cartilaginous in outer layer of stipe, soft inside, staining blue where bruised; odor and taste not recorded.

Spore deposit very deep brown, almost black.

Spores 8.5–10.5 × 7–8 × 5.5–6.5 μ, compressed, subelliptic in side view, rhombic to heart-shaped (angular ovate) in face view, with a truncate apex and a distinct germ pore, thick-walled, near bister when revived in KOH; basidia 4-spored, about 22 × 8 μ; pleurocystidia not seen in type; cheilocystidia 18–22 × 6–8 × 3.5–4 μ, fusoid-ventricose with obtuse apex, typically capped with a hyaline mucilaginous substance, the whole gill edge gelatinizing in KOH; pellicle of pileus distinct but formed by a thin layer of gelatinized epicuticular hyphae; clamp connections present.

On rotten wood. Buitenzorg, Java, Indonesia, *v. Höhnel*, TYPE (FH).

Although the species is lignicolous, the spores remind one of the coprophilous series. The presence of a distinct gelatinous pellicle separates this species from *P. subaeruginascens*. This was clearly demonstrated from a study of the types. The type of *P. subaeruginascens* is well dried, well preserved, and consists of fruiting bodies that were in prime condition when placed on the drier. Hence, the lack of a gelatinous epicutis is significant. The type of *P. aerugineomaculans* consists of two carpophores which were apparently over-age when dried and as preserved are inferior to quality to those of *P. subaeruginascens*. Under such circumstances one would expect the gelatinous pellicle, if one were present originally, to be pretty well obliterated. The fact that it is still present indicates to us that when fresh material is again collected the pellicle may be found to be rather thick and well developed.

From our comments on *P. subaeruginascens,* one might expect *P. aerugineomaculans,* no less than *P. subaeruginascens,* to occur in Japan.

The macroscopical descriptions of both Javanese species are adapted from Höhnel's notes.

STIRPS YUNGENSIS

4. PSILOCYBE YUNGENSIS Singer and Smith, Mycologia **50**: 142. 1958.

Var. YUNGENSIS (FIGS. 6–8, 45).

Pileus about 16 mm broad and equally high, margin at first incurved, conic with an obconic or button-like appendage at the tip, not expanding, deep rusty brown (*leaf mold*), in the marginal region between striae buffish gray (*cracker*), finely marked with long translucent striations when moist, somewhat viscid, staining deep blue (*39 H 5*) where injured.

Lamellae gray buff (*aloma*), with white edges, staining blue where wounded (*39 H 5*), very narrow, ascending and never becoming horizontal, crowded, adnate.

Stipe 55 mm long, 2 mm at apex, 3 mm at base, subequal, deep chestnut brown (*Hindu*), reaching *auburn* at apex, bluing less than cap and gills but such a change still evident, densely fibrillose floccose from light brownish fibrils on darker ground, becoming more fibrillose-pruinose toward apex, veil inconspicuous except for the floccons, no annulus formed.

Context concolorous with surfaces or somewhat paler both in pileus and stipe, moderately fragile in stipe; odor slightly raphanaceous.

Spore deposit dark lilac.

Spores 5–5.5 × 4.3–5 × 3.6–3.9 μ, compressed, dark olive sepia in KOH and NH_4OH, smooth, rhombic in face view and a hilar appendage visible, without suprahilar applanation or depression in side view, apical pore broad, wall thick and complex; basidia 13–18.5 × 4.7–6.2 μ, short-ellipsoid-clavate then elongating and finally ventricose in the middle 2-, 3-, or mostly 4-spored, hyaline; pleurocystidia present as an occasional cystidiole about the size of a basidium, but often with a low mucro, contents hyaline in KOH and not protoplasmatic; cheilocystidia 13–34 × 5–7.3 μ forming a sterile band along the edge, exceptionally variable: some clavate, some ventricose and with capitate to subcapitate apex, some ventricose above and constricted in the middle, others ventricose-fusoid and broadest in mid-portion, some ampullaceous, some capitate-cylindric, some subulate-sublanceolate, all hyaline, narrowest portions 2.7 μ or more; subhymenium of small irregular elements, not regularly arranged; with a brown to stramineous membranal pigment which often breaks up to incrust the walls of the cells; gill trama regular, consisting of elongate cylindric elements, pigmented like the subhymenium, with

0.8–1 μ thick walls; epicutis gradually more differentiated from the hypodermium toward the uppermost surface of the pileus, there often more or less gelatinized, with smooth hyaline filamentous elements subparallel, forming a cutis, ascending hyphal excrescences often present on these hyphae and some of these stramineous and incrusted; hypodermium of a compact layer of hyphae irregular in size and shape but generally repent and radially elongated, all strongly incrusted with ochraceous brown pigment; clamp connections present.

Chemical characters: KOH leaving a dark spot where dropped on any part of the carpophore; $FeSO_4$, no reaction.

In small to large groups on very rotten wood or humus containing decomposing woody material, in tropical-montane forest, fruiting in January (summer rainy season). Known only from the type locality, Cataratas de San Juán, road from La Paz to Coroico, Bolivia, 2000 m alt., 1–28–1956, *Singer B 648*, TYPE (MICH).

Var. DICONICA Singer and Smith, Mycologia **50**: 142. 1958. (FIG. 44)

Pileus as in the preceding variety but lower, with an acute papilla rather than a knob, not quite so long-striate and somewhat darker in color (*Mohawk*, and between striae *kis kilim*).

Lamellae sordid lilac or reddish brown (between *kermanshah* and *Rembrandt*), otherwise as in var. *yungensis*.

Stipe shorter than in the preceding variety.

Context odorless.

Spores 4.4–6.2(–7.2) × 3.8–5 × 3.3–3.8 μ, otherwise as in var. *yungensis;* basidia mostly 4-spored; pleurocystidia and cheilocystidia as in preceding variety; gill trama consisting of broad, often short, stramineous hyphae with thick walls; epicutis and hypodermium of pileus as in preceding variety; clamp connections present.

Chemical characters as in var. *yungensis*.

Gregarious on very rotten wood and humus in tropical-montane forest. Bolivia, Departamento La Paz, Provincia Nor-Yungas, Cataratas San Juán, 2000 m alt., *R. Singer B 651*, TYPE, 1–28–1956 (MICH).

The two forms designated temporarily as varieties come from the same place and were gathered the same day as separate populations. Each population had its own characteristic habit and color range as described above, but under the circumstances we did not think them sufficiently distinct to separate them specifically. They were considered "probably the same" when first collected in the field.

P. yungensis is a very strongly pigmented species with typically high, little or not expanding pileus but with originally incurved mar-

gin, and with a non-annular veil remaining in floccons on the surface of the thin stipe. The spores are different from those of all other species of this section.

STIRPS MEXICANA

5. PSILOCYBE MEXICANA Heim, Rev. de Mycol. **22**: 77. 1957. (FIG. 25–26, 43)

Pileus 5–33 mm broad, 4–15 mm high, conic-campanulate and usually with a central papilla, frequently becoming hemispheric to convex and sometimes papillate in addition, broadly conic in others, and becoming umbonate and in these the umbo sometimes crowned by a papilla, always relatively high and narrow and not fully expanded, eventually, however, often convex with an uplifted margin, glabrous, viscid but soon dry, margin at times sulcate-striate to a small apical smooth disc, disc deep ochraceous to ochraceous brown, then fulvous, marginal zone much paler, hygrophanous, fading to ochraceous over the disc, gray brown in marginal zone and pale ocher-gilvous between, all traces of silky white veil soon vanishing from the margin.

Lamellae pale gray, eventually deep sepia, close to subdistant, ascending to almost horizontal, adnate to adnexed, only moderately broad, edges whitish.

Stipe 20–80 × 1–3 mm, hollow, equal and elongate, sometimes rather distinctly attenuated at the base, ochraceous, at maturity the apex paler, central portion often fulvous, glabrous when mature; veil thin and leaving fine appressed silky fibrils on the upper third, soon evanescent.

Context in pileus paler than surface, turning blue when bruised or on drying; odor always rather strongly farinaceous; taste slightly disagreeable.

Spore deposit deep sepia to dark purple brown.

Spores (7.7–)8.8–10.5(–12) × (5.5–)6.7–7.7 × (5–)5.5–6.7 μ, compressed, in face view elliptic to rhombic and then broadest in midportion, subelliptic in side view, dingy yellowish brown in KOH, smooth, with thick walls, furnished with a distinct broad germ pore; basidia 20–32 × 6.3–7.7 μ, 4-spored, variable in size, typically with a median or more superior constriction; pleurocystidia none, or a few similar to cheilocystidia near the edge; cheilocystidia forming a sterile band along edge, 15.5–30.5 × (3–)4–9 μ, usually short pedicellate, hyaline, fusoid-ampullaceous, the neck short (rarely long), apex obtuse to acute (rarely capitate or bifurcate); subhymenium a thin layer of very irregular small elements; hymenopodium of relatively narrow filamentous axially arranged parallel hyphae, layer thin; gill trama regular, hyaline to stramineous, with voluminous (up to 19 μ in diameter) elements, hyphal walls up to 1.5 μ in diameter; epicutis a broad

hyaline layer of filamentous mostly hyaline hyphae, not strongly gelatinized but well differentiated from hypodermium, hyphae 1.7–3.5 μ in diameter; hypodermium a colored (yellowish brown) layer of hyphae 2–14 μ in diameter, with pigment in the walls (not incrusted); body of context hyaline to yellowish, many hyphae up to 20 μ in diameter and walls up to 1.5 μ thick; dermatocystidia none; clamp connections present.

On the earth or on plant fragments such as mulch from sugar cane presses, usually in open fields and springy meadows, never on dung; always solitary but often in large numbers in a limited territory; fruiting from May until October, common in the transition zone between the tropical-montane and the temperate-montane zone—*i.e.*, between 1500 and 1800 m alt.—favoring limestone regions. Reported from Southern Mexico and Guatemala.

Illustrations: Wasson, Mushrooms Russia and History **2**: *pl. 40, fig. 1;* Life, May 13, 1957, p. [107], *fig. at lower left.*

Material studied: Mexico: Oaxaca, Huautla de Jiménez, *R. G. Wasson 3,* 13–8–1953 (NY); *R. Singer M 1502,* July 10, 1957 and *M 1521,* July 11, 1957 (both MICH).

This is the only mycenoid representative of the genus occurring in Oaxaca and consequently the only mycenoid hallucinogenic mushroom used by the Mazatecs. For this reason it is sometimes confused with *Panaeolus sphinctrinus* which has a similar habit but is more obtuse, with blacker lamellae, and grows mostly directly on dung.

STIRPS SILVATICA

6. **Psilocybe silvatica** (Peck) comb. nov. (FIGS. 27, 29).

Psathyra silvatica Peck, Ann. Rep. N. Y. State Mus. **42**: 20. 1889.
Hypholoma silvaticum (Peck) A. H. Smith, Contrib. Univ. Mich. Herb. **5**: 21. 1941.

Pileus 8–25 mm broad and at least half as high, obtusely conic to campanulate, margin straight at first, disc often with a papilla, glabrous, viscid, shining when dried, tawny to rather dark brown, hygrophanous, fading to pale ochraceous buff to grayish melleous or grayish brown.

Lamellae dull ferruginous brown when mature, narrow to broad, adnate, ascending to almost horizontal, close to subdistant, with a pallid edge.

Stipe 20–80 × 1–3 mm, equal or slightly thickened at the base, tubular, flexuous, pallid to brownish, apparently whitish from a superficial appressed fibrillose covering, this layer thinning out downward

and more brown showing through from cortex of the stipe; veil apparently very weakly developed and all traces gone in mature specimens.

Context in pileus membranous and fragile, in stipe brownish and cartilaginous; taste farinaceous; odor also farinaceous (from crushed flesh).

Spores in deposit "benzo brown" (violaceous brown).

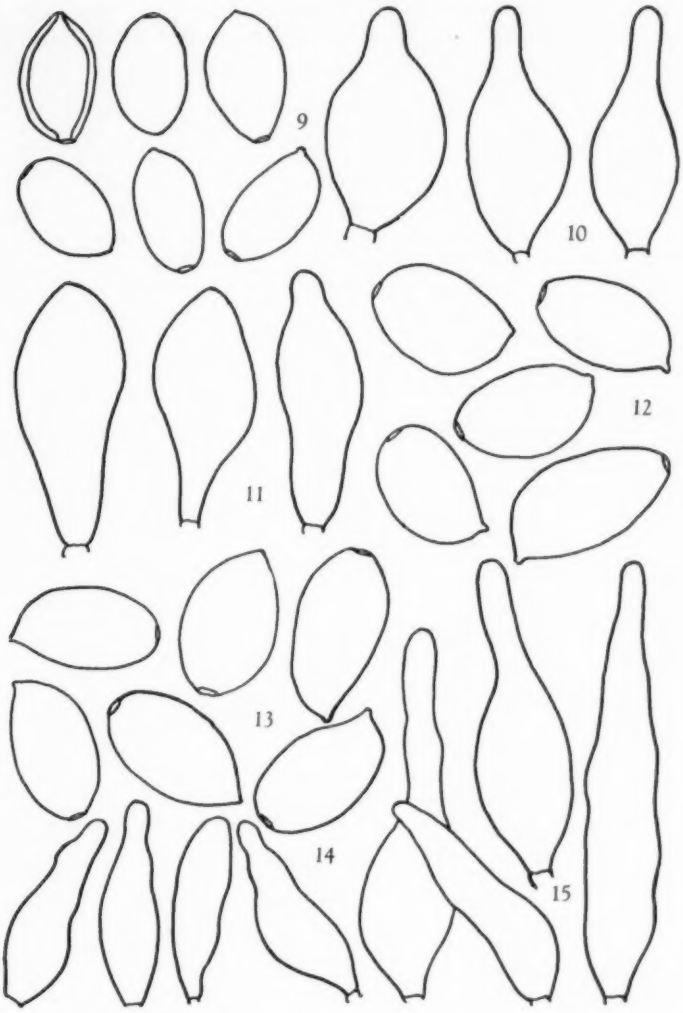
Spores 6–9.5(–11.5 from 2-spored basidia) × 4.5–5.5 μ, dingy yellowish brown in KOH, smooth; with a complex thick wall, terete in cross section, with a distinct apical germ pore; basidia 19–27 × 5.7–8 μ, 4-spored, rarely 2-spored; pleurocystidia none; cheilocystidia 24–45 × 4–10 μ, ventricose below and often ampullaceous with an elongated neck 1.3–2.2 μ thick, tapering to an obtuse to (rarely) subacute apex, often pedicellate, forming a sterile band on gill edge; subhymenium thin, melleous in KOH; gill trama of relatively broad hyphae with walls up to 0.8 μ thick, pale melleous in KOH and lacking pigment incrustations; epicutis of pileus a thin pellicle of gelatinized hyaline to yellowish filaments 1–2.8 μ in diameter, but pellicle not very strongly gelatinous; hypodermium of compactly arranged hyphae 3 μ or more broad and more highly pigmented than in trama proper, pigment incrusting the walls; clamp connections present.

In small groups, gregarious but not cespitose, in the woods on debris around stumps or on leafmold (mostly *Fagus grandifolia*), generally not directly on stumps or logs, fruiting in September and October. Known from New York, Ontario, and Michigan.

Material studied: U.S.A.: New York, Star Lake, *Peck*, PARATYPE of *Hypholoma fragile* (NYS); North Elba, *Peck*, TYPE (NYS). Mich., Milford, *Smith 20970*, 10–4–1949 (MICH). CANADA: Ont., Bear Island, Lake Timagami, *Smith 4777*, 9–9–1936 (MICH).

Hypholoma fragile was originally reported by Peck from two localities, Star Lake and Painted Post, both in New York. As A. H. Smith (**18**) previously pointed out, the Painted Post collection should be regarded as the type. This latter is a *Psathyrella* and the same as *P. hymenocephala* (Peck) Smith. The Star Lake collection is *P. silvatica* (Peck) Sing. & Sm.

When A. H. Smith (**17**) described *P. pelliculosa* the confusion involving *H. silvaticum* had not been discovered. After working out the details of this problem he considered the apparently slight differences existing between *P. pelliculosa* and *P. silvatica* as of no taxonomic significance and reduced *P. pelliculosa* to synonymy with *P. silvatica*. It now appears from the study of all known species in this section that the slight differences disregarded earlier may have taxonomic significance and so *P. pelliculosa* is re-established here.



FIGS. 9–15. 9: spores of *Psilocybe aztecorum*. 10: cheilocystidia of *P. collybioides*. 11: pleurocystidia of *P. collybioides*. 12 and 15: spores and cheilocystidia of *P. strictipes*. 13: spores of *P. baeocystis*. 14: cheilocystidia of *P. candidipes*.

7. **Psilocybe pelliculosa** (Smith) comb. nov. (FIGS. 28, 30, 42).
Psathyra pelliculosa A. H. Smith, Mycologia **29**: 58. 1937.

Pileus 8–15(–30) mm broad, at least half as high as broad, obtusely conic with a straight margin when young, remaining so or becoming more broadly conic-campanulate, never fully expanding, surface glabrous, smooth, viscid from a separable gelatinous pellicle, hygrophanous, "Saccardo's umber" to "Isabella color" (dark dingy yellow-brown or more olive showing), usually fading to "pinkish buff" (dull pale alutaceous), often with greenish gray tints in age, margin translucent-striate when moist.

Lamellae dull "cinnamon brown" until darkened by the spores, adnate but eventually separating from the apex of the stipe, rather narrow to moderately broad, markedly ascending at first, less so in age, close, edges pallid.

Stipe 60–80 mm long, 1.5–2 mm thick at apex, equal above an enlarged base (base enlarged from adhering debris), pallid to grayish, appressed silky fibrillose and brownish below and reaching bister in age, pruinose above; veil absent to rudimentary.

Context thin and pliant in pileus, rather tough in stipe, turning slightly bluish or greenish where injured in pileus and stipe; odor none or slightly musty.

Spores 9.3–11 × 5–5.5 μ to 10.5–13(–14) × 5.5–7 μ (according to populations, all 4-spored), dark yellow brown in KOH, showing a distinct apical germ pore (often convex), smooth, terete, ellipsoid to subovoid; basidia 4-spored, 22–30 × 7–8 μ, hyaline; pleurocystidia none or only near gill edge and similar to cheilocystidia; cheilocystidia 22–36 × 5.5–7.5 μ, hyaline, forming a sterile band on gill edge, often pedicellate, fusiform-lanceolate with an elongated neck tapering to an acute to subacute apex, neck rarely cylindric with an obtuse apex, hyaline in KOH; subhymenium narrow and irregular, brownish in KOH; gill trama regular, pale brownish in KOH; epicutis of pileus a thick pellicle of more or less horizontal very loosely arranged strongly gelatinized wavy hyphae 0.8–5.5 μ in diameter, hyaline, walls never incrusted; hypodermium of compactly subparallel hyphae tawny from having colored walls but walls not incrusted; all hyphae with clamp connections.

Scattered to gregarious or cespitose on debris and humus in and near conifer forests from September to December. California, Oregon, Washington, Idaho.

Illustration: A. H. Smith in Contrib. Univ. Mich. Herb. **5**: *pl. 10, fig. 1* (*Hypholoma silvaticum*). 1941.

Material studied: Idaho: Granit Creek, Nordman, *A. H. Smith 54268*, 10–8–56 (MICH). Washington: Lake Cushman, Olympic Mts., *C. H. Kauffman*, 10–11–15 (*Psathyra fagicola*) (MICH); Lake

Quiniault, *C. H. Kauffman,* 10–13/27–25 (all three MICH); Lake Crescent, *A. H. Smith 3074,* 10–10–35 (MICH); numerous other collections from nearby places in Washington: *A. H. Smith 3196, 17875, 39887, 40212, 40465/6, 40526, 40966, 41181, 49088, 49381;* Zenith, *J. B. Flett,* 11–3–41 (all MICH). Oregon: Near Lake Tahkenitch, *A. H. Smith 3431,* 11–11–35, TYPE (MICH); other Oregon collections, *A. H. Smith 3461, 7893, 9298, 25057, 49488* (all MICH). California: Crescent City, *A. H. Smith 8260,* 10–30–37 (MICH).

STIRPS CYANESCENS

8. PSILOCYBE AZTECORUM Heim, Rev. de Mycol. **22**: 78. 1957 (FIGS. 9, 31).

Psilocybe mexicana var. *longispora* Heim, C. R. Acad. Sc. **244**: 1393. 1956, nom. subnud.

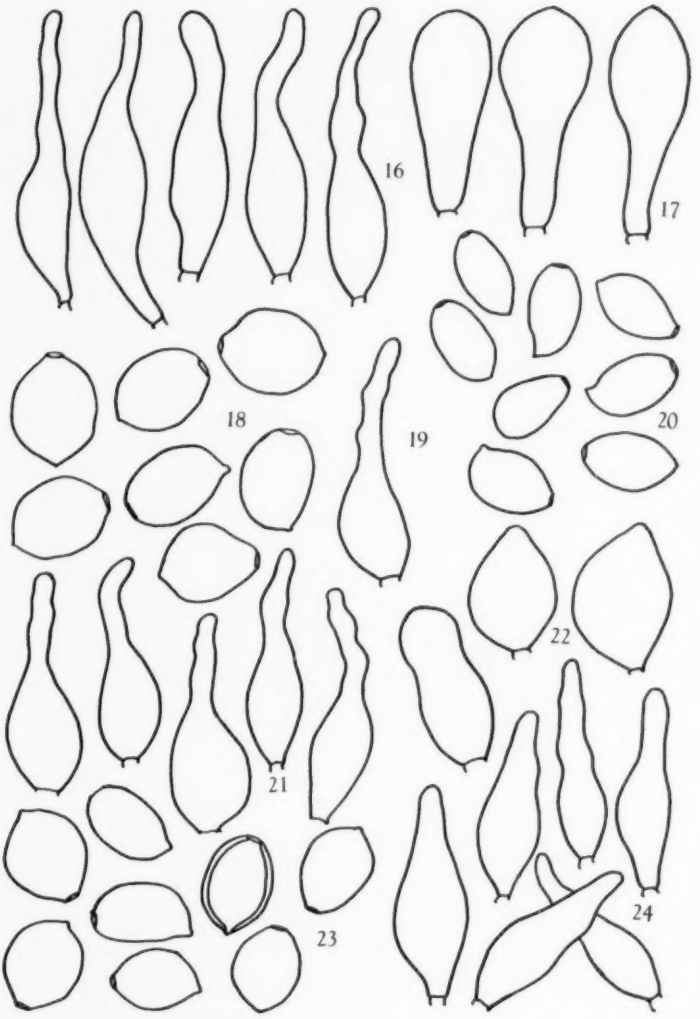
Pileus 15–25 mm broad, obtuse to subumbonate, expanding to broadly conic or campanulate, glabrous except for traces of the veil along margin at first, slightly viscid, hygrophanous, milk white with yellowish disc, striate over about a third of the radius when moist, pale buff faded, disc tending to become rimulose-cracked in some specimens.

Lamellae deep purple brown when mature, adnate, broad, fairly close, with pallid to whitish edges.

Stipe 30–60 mm long, 2–4 mm thick at apex, equal or nearly so, fibrous, base at times enlarged, often flexuous, whitish, staining blue, becoming grayish on discolored portions, especially over lower part in age; veil well developed, sometimes forming a fugacious annulus.

Context white, changing to blue readily, especially in the stipe; odor farinaceous; taste astringent.

Spores 10.5–14(–16.2) × 5.3–7.7(–8.8)μ, elongate-ellipsoid, terete, revived in KOH dark dull ochraceous brown with olive tone and a red brown line showing along the endosporium, thick-walled, germ pore broad and distinct, wall smooth; basidia hyaline to melleous-hyaline, mid-portion usually constricted, 24–31 × (5–)7.7–10(–10.5)μ, (1-, 2-, 3-)4-spored, sterigmata 6–6.5(–7.8)μ long; pleurocystidia similar to cheilocystidia, rare to scattered, rarely a few cystidioles found, their shape reminding one of one-spored basidia; cheilocystidia abundant, causing gill edge to be heteromorphous, 24–45 × 5–8 μ, fusoid-ampullaceous with filamentous neck, neck rarely tapered sharply to a subacute apex, 6–11 μ long and about 2.5 μ in diameter; pilocystidia none; caulocystidia abundant near apex of stipe, variable in shape, 17–43 × 4–9 μ, ventricose at base and with or without a short neck; epicutis a thin pellicle consisting of narrow (1–2.2 μ) gelatinized hyphae hyaline in KOH; hypodermium poorly differentiated but hyphae up to 14 μ broad,



FIGS. 16–24. 16: cheilocystidia of *Psilocybe bacocystis*. 17 and 20: pleurocystidia and spores of *P. candidipes*. 18, 19, 21: spores, pleurocystidia and cheilocystidia of type of *P. caerulescens*. 22–24: pleurocystidia, spores and cheilocystidia of *P. mazatecorum* (Mexican specimens so determined by Heim) = *P. caerulescens*.

having colored (non-incrusted) walls and not gelatinized; clamp connections present.

In small groups on the earth in open pine woods (*Pinus hartwegii*), associated with grasses and *Alchemilla procumbens*. It fruits in September and is known only from around Paso de Cortés, Mexico and Puebla, between 3300 and 3700 m elevation, Mexico. *G. Guzmán VA 1099*, September 1957, TOPOTYPE (MICH).

Illustrations: Singer, Chicago Nat. Hist. Mus. Bull. Dec. 1957 (photo); *Life*, May 13, 1957, p. [106], *upper fig.*

In this species are combined the characters of small carpophore size, large spore size, and fairly copious veil development. It is only slightly —never abundantly—pigmented, but the fact that it turns blue when injured has been very clearly established by G. Guzmán on the material on which our description is based, and the local inhabitants likewise consider the bluing one of the mushroom's characteristic features.

9. PSILOCYBE CYANESCENS Wakefield, Brit. Mycol. Soc. Trans. **29**: 141. 1946.

Pileus 20–40(–75) mm broad, convex, becoming expanded, viscid, hygrophanous, when moist chestnut color, fading yellowish or ochraceous, margin striate when moist, staining blue when touched.

Lamellae cinnamon colored becoming badio-fuscous as spores mature, adnate to adnate-decurrent, subdistant, up to 5 mm broad, edges paler.

Stipe 60–80 × 2.5–5 mm (rarely 100 × 7 mm), fairly rigid, base somewhat enlarged and often curved near the base, whitish, silky fibrillose, changing to blue when bruised or in drying; veil cortinate, snow white and thin, best seen on young fruiting bodies.

Spore print fuscous.

Spores 9–12 × 5.5–8.3 × 5–7.7(–8) μ, mostly slightly broader in face than in side view, smooth, nearly elliptic in side view, more ovate in face view, with a distinct broad apical germ pore, wall thick and complex, dingy yellow-brown in KOH and with a reddish chestnut line along the endosporium; basidia 4-spored, 16–26 × 7.2–9.3 μ, cheilocystidia 12–26 × 5–8 μ, fusoid-ventricose, with the neck 2–4 μ thick and projecting about one-third of the total length of the cheilocystidium, apex obtuse; pleurocystidia few, in form of cystidioles, 21–28 × 5.5–8.8 μ, resembling basidioles but mucronate and lacking both protoplasmatic granulation and refractive internal body when revived in KOH (hence neither basidioles nor chrysocystidia); gill trama regular, hyaline to melleous, the hyphae lacking pigment incrustations and having thin to moderately thickened walls; epicutis a pellicle of long loosely arranged

filaments imbedded in a gelatinous mass; beneath this a hypodermium of melleous but not conspicuously incrusted hyphae; pilocystidia none; clamp connections present.

On the earth among leaves and dead twigs in woods, perhaps occasionally on rotten wood, known only from Kew Gardens, Surrey, England, TYPE (K).

The description of the field characters is translated from the original description. The data on microscopical characters were obtained by us from a study of the type.

It is not impossible that this species was introduced to Europe with exotic plant material.

10. PSILOCYBE COLLYBIOIDES Singer and Smith, Mycologia **50**: 141. 1958. (FIGS. 10–11.)

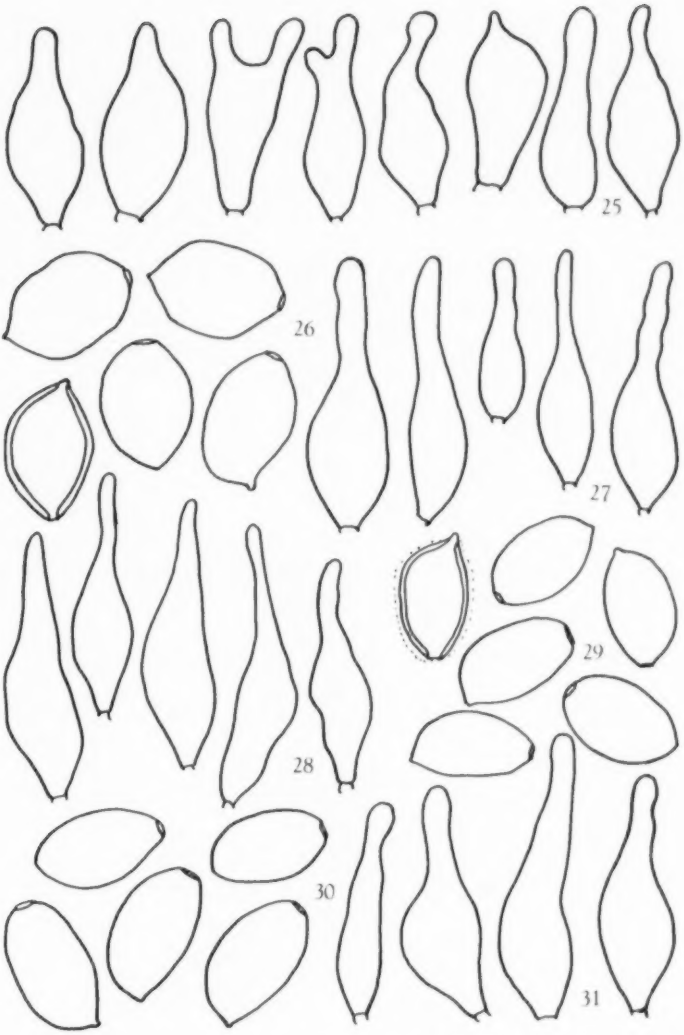
Pileus 13–40 mm broad, at first campanulate and often soon varying toward convex, at maturity convex or retaining a more or less elevated umbo, eventually tending to become flattened and irregular, surface glabrous, viscid when moist, somewhat hygrophanous, when moist usually finely translucent striate and more sordid-pallid all over, faded light ochraceous brown (*13K 9*) with dingy pallid center, discoloring (where touched and on drying) from the center outward and finally reaching *bottle green* or *bayou*, often with a short sulcate margin.

Lamellae pallid to pure white, in some slightly brownish at maturity, close or subclose, more or less adnate, moderately broad to broad (e.g., 2.5 mm).

Stipe 30–70 × 1.5–4.5 mm, equal to slightly thickened downward, often twisted-contorted, curved, compressed, knotty or variously irregular, stuffed becoming hollow, white at first, often becoming cinnamon-brown from the base upward, at times remaining white or fading out to white again in age, when young silky fibrillose and sometimes subsquamulose from the veil, later appressed finely fibrillose, apex fibrillose-pruinose; veil cortinate-fibrillose, white, fugacious; basal mycelium sometimes strigose, white, and forming white rhizomorphs.

Context white to pallid or in parts cinnamon, always discolored under the cuticle and in cortex of stipe, turning green to blue (*bottle green* or *bayou*) when injured, fleshy in pileus, somewhat tough in stipe; odor slightly farinaceous becoming spermatic.

Spores generally none, or few, typical of the Strophariaceae, about 10 × 6.5 μ (hymenophore nearly sterile or sterile); basidia not seen; pleurocystidia in form of cystidioles forming the hymenium, hyaline, some 24–32 × 7.3–9.5 μ, attenuate above and often with a rounded mucro, others more pseudoparaphysoid, vesiculose to broadly clavate, 14.5–23 × 9.3–13 μ; chrysocystidia none; cheilocystidia abundant, caus-



FIGS. 25–31. 25–26: cheilocystidia and spores of *Psilocybe mexicana*. 27 and 29; cheilocystidia and spores of *P. silvatica*. 28 and 30: cheilocystidia and spores of *P. pelliculosa*. 31: cheilocystidia of *P. aztecorum*.

ing the gill edge to be heteromorphous, 17–23.5 × 8–9 μ, fusoid-ventricose with narrow (1.5–2 μ) extended neck and with obtuse to capitate (and then up to 3.5 μ diameter) tip; subhymenium consisting of irregular very small elements; hymenophoral trama regular, its hyphae with about 0.5 μ thick walls, without membrane-pigment; epicutis a pellicle consisting of loosely arranged gelatinized hyphae, hyaline in KOH; hypodermium of nearly non-pigmented hyphae, or in some a slight amount of wall incrustation (melleous) present, especially in young non-contorted carpophores; clamp connections present.

On dry slopes over loose gravel near *Alnus jorullensis* var. *spachii* and on various types of organic debris (humus, grass culms, semi-decomposed alder leaves, etc.) in semi-shade, gregarious, fruiting in the summer rainy season (February), Argentina, prov. Tucumán, Pre-Andine Sierras, Tafí del Valle, 2000 m altitude, *Singer T 1882*, TYPE (MICH).

The above collection was designated type in order to leave open the question of the identity of the North African species whose description follows, even though the latter and the type appear to be the same. If the North African species is not the same as ours it will have to be renamed because the epithet *cyanescens* is preoccupied in *Psilocybe*. The Argentine species described above has the appearance of a *Collybia*, hence the specific epithet proposed.

Description of Maire's sterile to semi-sterile material from Algeria

The following description of *Hypholoma cyanescens* R. Maire, Bull. Soc. Mycol. Fr. **44**: 51. 1928, refers to a North African species which we think probably identical with *P. collybioides*. This description is adapted from the original diagnosis. We have seen no specimens.

Pileus 15–30 mm broad, convex, then expanding, not umbonate, viscid and with a separable glutinous pellicle, hygrophanous, dingy ochraceous, faded pallescent, margin faintly striate or not striate.

Lamellae whitish becoming dingy and pallid ochraceous, finally light rufous-fuscous, close, thin, narrow (1.5–2.5 mm), arcuate, somewhat rounded behind and narrowly attached (rounded-adnexed), not intervenose, lamellulae attenuate, edges whitish pruinate.

Stipe 25–40 × 2–5 mm, subequal or slightly enlarged below, stuffed with a white silky medulla, eventually tubular, whitish, apex pruinose, innately fibrillose downward; cortina cobwebby, white, fugacious.

Context slightly fulvous, fulvous in the base of the stipe, faded pallescent, white in the stuffing of the stipe, bluing in all parts of trama on injury; odor raphanaceous; taste mild.

Spore deposit purple-brown.

Spores 10–12 × 5.5–6.5 μ, from 4-spored basidia, occasionally up to c. 20 × 7.5 μ from 2-spored basidia, ellipsoid, light fuscous brown, rather thick-walled, smooth, with a rounded to slightly attenuated apex furnished with a germ pore; basidia clavate, 4-spored, few 2-spored, 28–32 × 7–9 μ; pleurocystidia none or rare and similar to cheilocystidia; cheilocystidia 30–40 × 6–8 μ, fusiform with a subcylindric ampullaceous neck and an apex incrusted with calcium oxalate; subhymenium thin, ramose; gill trama regular, its elements 5–8 μ in diameter and rather long, interwoven.

Chemical characters: guaiac solution negative; NH_4OH negative.

Gregarious under *Cedrus atlantica*, fruiting from October until December. Algeria, Blida and La Chréa.

Description of fertile material referred to Hypholoma cyanescens by Malençon

The following description is translated and adapted from Malençon (**8**):

Pileus 15–35 mm broad, almost spheric to convex becoming campanulate to conic-campanulate, the margin finally spreading, viscid from a separable gelatinizing pellicle, naked, hygrophanous, ochraceous then amber yellow with a bister shade, finally dusky olive, bister, fading from the disc outward to yellowish white or dull stramineous ("as if it were gouachée"), in age at times disc leather color, translucent-striate half way to disc when moist, opaque when faded.

Lamellae pale argillaceous becoming more lilac-beige, eventually dark purple brown, thin, not close, narrow, ascending, free to slightly adnexed, with white fimbriate edges.

Stipe 50–70 × 2–3 mm, equal to a slightly thickened base, solid becoming fistulose with a slight silky stuffing, pruinose on apex, lower down with a thickish coating of silvery to yellowish appressed fibrils; cortina silvery white, fugacious; basal mycelium cottony white, agglutinating, long white rhizomorphs present.

Context watery, with an amber color tone, lower part of stipe amber, thick in disc of pileus, thin toward margin, rather rough in stipe, changing green to blue where injured; odor and taste none.

Spore deposit blackish purple fresh, blackish in the herbarium.

Spores (11–)11.25–13(–13.5) × 5.5–7 μ, most frequently 11.2–11.8 × 5.5–6.25 μ, almond shaped, smooth, thick-walled, violet in water mounts, yellow brown in NH_4OH, apical germ pore obliterated by a hyaline callus; basidia 30–35 × 8 μ, 4-spored, cylindric or constricted, sterigmata 5 μ long; cystidioles (?) piriform, 15–17 × 7.5–8.5 μ; pleurocystidia (other than cystidioles) none or similar to cheilocystidia and near gill edge; cheilocystidia 30–40 × 6–8 μ, abundant (edge heteromorphous), ampullaceous and neck often incrusted with a spherical

collar, walls hyaline; subhymenium cellular (?); hymenopodium of thinner more parallel hyphae than the hymenophoral trama proper which consists of broad hyphal cells narrowed at the septa; apex of stipe with numerous dermatocystidia similar to cheilocystidia; pellicle of pileus of interwoven gelatinized hyphae, with those of the extreme surface often diverticulate as in some *Mycenae;* hypodermium filamentose.

Often on small pieces of dead wood but also on the ground, fruiting from October until November in the *Cedretum* (*atlanticae*) and *Quercetum* (*ilicis*) above Azrou, Morocco.

In order to represent the facts as free from possible misinterpretation as we reasonably could, we have presented the data available on the collections made by each author. Experience with numerous sterile forms in the genus *Naematoloma* in North America has shown that in these the colors invariably have more yellow in pileus, lamellae, and stipe than do those of normally fertile carpophores, but that there is no correlated variation in spore size and shape. Hence, as long as these characters can be obtained from semi-sterile forms, they can be used in classifying collections. We do, however, believe that in interpreting differences in color, especially as the yellow pigments are concerned, it is best not to attempt fine distinctions between collections in situations such as this one. Also we cannot regard semi-sterility in itself as necessarily being a legitimate species character.

We believe that all of the material on which the descriptions presented here are based belongs in a single species. Spore characters are essentially the same, as are the characters of the cheilocystidia and lack of pleurocystidia. There may be some differences in odor and taste but in no case are the characters pronounced enough to be convincing in view of the small amounts of material tested.

Since the specific epithet *cyanescens* cannot be transferred to *Psilocybe* because of the existence of *P. cyanescens* Wakefield, we are describing the South American material as a new species and designating a type from that region. By doing this we do not prejudice the situation as far as future studies of the African populations are concerned. If some of the slight differences noted in the descriptions presented here are found to be important, adjustments in the classification can then be made. There is the possibility that Malençon's collections are conspecific with Miss Wakefield's *P. cyanescens.*

11. PSILOCYBE STRICTIPES Singer & Smith, Mycologia **50**: 141. 1958. (FIGS. 12, 15, 50.)

Pileus 20–40 mm broad, when young campanulate to convex, becoming broadly convex to plane or with an elevated wavy margin in age,

glabrous, viscid from a separable pellicle, margin striatulate when moist, hygrophanous, dull yellowish brown to olive brownish ("Isabella color"), fading to cinnamon buff on disc and pallid on margin, becoming dingy over all in age, where bruised staining greenish or bluish green.

Lamellae pallid becoming dark chocolate color from the spores, bluntly adnate to depressed-adnate, horizontal, narrow (4 mm in a 40 mm cap), close but not crowded, with three tiers of lamellulae.

Stipe 100–130 × 2–3 mm, straight, equal or slightly flared at apex, stuffed with a pallid brownish pith, staining brownish where outer fibrils have been removed, surface pallid from appressed fibrils, often zoned near apex from broken veil, with fibrils over lower half and strigose hairs at base, staining bluish green.

Context concolorous with surface in pileus, dingy brownish and cartilaginous in the cortex of the stipe; odor none; taste mild.

Spore deposit purplish.

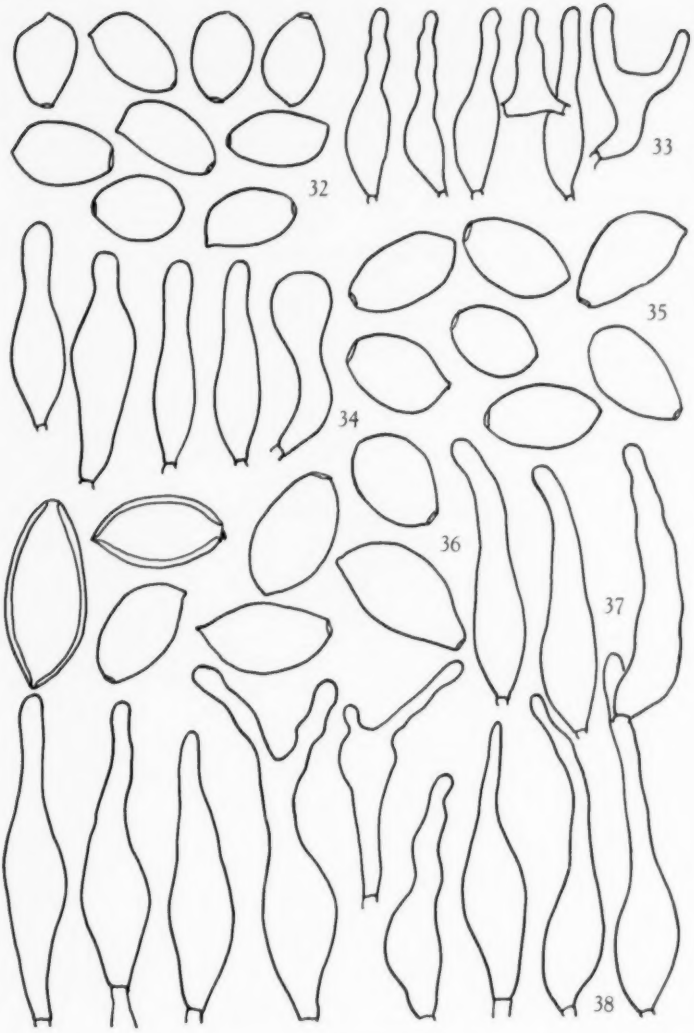
Spores 9–12(–12.7) × 5.5–6.5 μ, smooth, with a distinct apical germ pore, oblong in face view, slightly inequilateral in side view, sordid tawny in KOH; basidia 25–31 × 7–9 μ, 4-spored, clavate or subcylindric with a median constriction, projecting when sporulating; hymenium dull rusty brown to pale yellowish in sections revived in KOH; pleurocystidia none or only near gill edge and similar to the cheilocystidia; cheilocystidia 26–45 × 6–12 μ, abundant, causing gill edge to be heteromorphous, hyaline, ventricose below, subulate, attenuated gradually towards the subacute to obtuse tip; gill trama of enlarged cells pale sordid brownish to hyaline (paler than hymenium in KOH); epicutis a thick gelatinous pellicle of hyaline narrow (1.5–3.5 μ) hyphae; hypodermium of broad (3–10–18 μ), somewhat interwoven hyphae, pigmented but almost as pale as the flesh beneath, not incrusted; clamp connections readily demonstrated.

Subcespitose on wood of conifers and debris in coniferous and mixed woods, fruiting in October, Oregon, U.S.A.

Material studied: Oregon: near Welches, *Gruber & Smith 20248*, TYPE (MICH). Other specimens from the same general region: *Smith 24622, 24403* (MICH). (No. 202448, indicated as the number of the type in the original diagnosis, is erroneous.)

12. PSILOCYBE BAEOCYSTIS Singer and Smith, Mycologia **50**: 141. 1958. (FIGS. 13, 16.)

Pileus 14–54 mm broad, appearing umbonate when dried but conic when fresh and with incurved margin, finally expanding to convex or plane, viscid from a thin gelatinous pellicle, olive brown to buffy brown, when dried tending toward copper brown in the center, with a faintly striate margin when moist, finally with a greenish fringe around the margin and becoming greenish where touched.



FIGS. 32–38. 32–33: spores and cheilocystidia of *P. aggericola*. 34–35: cheilocystidia and spores of *P. muliercula*. 36–38: spores and cheilocystidia of *P. caerulipes*.

Lamellae dark cinnamon or gray, also with faint purplish tints in some, eventually nearly "heliotrope gray," adnate to uncinate, subclose, edges whitish.

Stipe 50–70 × 2–3 mm, equal to subequal, stuffed with loose fibrils, with fine white fibrils on surface, white except for apex which is yellowish; veil present but inconspicuous.

Context concolorous or paler than surface in pileus, brown in stipe; odor and taste none.

Spore deposit "heliotrope gray."

Spores (8–)10–13.3 × 6.3–7 μ (mostly 11–12 × 6.3–7 μ), terete or nearly so, with a broad distinct germ pore, deep olive to dingy brownish olive-yellow in KOH, smooth, wall very thick and complex, with a suprahilar depression or applanation; basidia 20–30 × 7–9 μ, 4-spored, hyaline to stramineous; pleurocystidia none; cheilocystidia 20–30(–36) × 4.2–5.7 μ, ampullaceous with a long thin neck (1.2–1.5 μ diameter) and subacute apex, or more often ventricose below or in middle but then pedicellate and tapered to an acute apex, hyaline, causing gill edge to be heteromorphous; subhymenium a rather broad and irregular layer of small versiform elements, slightly pigmented; hymenopodium a thin filamentous layer, regular, not as well separated as in some other species; gill trama hyaline, regular, with a slightly and indistinctly differentiated mediostratum and this flanked by parallel hyphae on either side, progressively more pigmented in the third of the trama closest to the pileus trama; epicutis a very thick hyaline gelatinous layer of narrow loosely arranged hyphae; hypodermium weakly to strongly pigmented, consisting of compactly parallel horizontal hyphae broader than those of the epicutis; clamp connections regularly present.

On decaying "peat moss" (actually apparently a mixture used instead of pure *Sphagnum*) by a green house, Eugene, Oregon, U.S.A., *F. P. Sipe*, 11–1–1945, TYPE (MICH).

This is somewhat similar to *P. strictipes* and may be confused with it, but differs in the size and shape of the cheilocystidia, which are reminiscent of those of *P. caerulipes*.

STIRPS CAERULESCENS

13. PSILOCYBE CAERULESCENS Murr., Mycologia **15**: 20. 1923 (FIGS. 18, 19, 21–24, 46, 48.)

Psilocybe mazatecorum Heim, C. R. Acad. Sc. **242**: 1392. 1956, nom. subnud.

Psilocybe caerulescens var. *mazatecorum* Heim, Rev. de Mycol. **22**: 78. 1957.

Pileus 20–88 mm broad, at first obtusely campanulate, becoming convex with a decurved margin, at times slightly umbilicate or with a small

umbo, rarely becoming irregular and almost plane or shallowly depressed in age, almost black or very deep olive-umber at first, becoming paler and olive tinge often disappearing, in age often rather pale colored (near *aztec*), umbo either darker than marginal area or at times paler, hygrophanous, fading gradually to ochraceous from disc outwards, sometimes assuming chestnut or fulvous colors in the moist areas while still fading (see illustrations by Wasson), and these at times persistent in the faded specimens, a brownish shade often pervading the disc, glabrous, smooth, slightly viscid to lubricous, short striate by translucence in smaller caps or striate half way to disc in large ones when moist, opaque when faded; veil usually fugacious on pileus, but sometimes more persistently white appendiculate.

Lamellae mostly light avellaneous gray or argillaceous, only in age reaching sepia, sinuate-adnate to bluntly adnate, close to subclose, broad, edge slightly white fringed.

Stipe 40–122 × 2–10 mm, typically equal, hollow, glassy-white to sordid although at first always with a continuous white velutinous soft covering which soon breaks up into a marbled to flocculose covering on a sordid ground color, the apex pallid fibrillose, glabrescent; basal mycelium white, occasionally developing some white rhizomorphs which at times turn blue when injured; veil thin and at first appearing cortinoid, pure white, often forming a ring for a very short time in young or nearly mature specimens, not distinctly bluing.

Context of pileus whitish to sordid or even tawny to fulvous, sometimes dark brown in upper portion of pileus, fleshy, somewhat fibrous-hard in stipe, blue when injured; odor strongly farinaceous; taste astringent.

Spore deposit deep purple fuscous, sepia.

Spores (6–)6.3–7.7(–8) × 5–6 × 3.5–5 μ, compressed, 0.5–1 μ narrower in side than in face view, varying from subrhombic with rounded angles to ovate in face view, and from elliptic to inequilateral in side view, deep yellowish brown in KOH, smooth, with a broad germ pore, wall thick and compound as revived in KOH, showing a rusty line along the endosporium, without a suprahilar depression but at times with a small applanation; basidia (12–)14–21 × 4.9–7 μ, 4-spored, rarely 2-spored; pleurocystidia none except for some permanently sterile basidioles (?) or a few cells resembling the cheilocystidia; cheilocystidia 15–20(–26) × (3–)4–5.5(–6) μ, hyaline, fusoid to fusoid-ampullaceous, the apex acute to slightly enlarged, neck sometimes flexuous to filamentous and 1.5–2 μ in diameter; subhymenium a narrow layer of irregular short elements, melleous to hyaline as revived in NH_4OH; hymenopodium hyaline, consisting of parallel filamentous hyphae; the hymenophoral trama proper consisting of a lateral stratum of broad (7–11 μ diameter) hyaline hyphae accompanying the mediostratum on

both sides, and the mediostratum consisting of a mixture of broad and narrow (2.5–3 μ) hyphae, walls of all cells 0.3–0.4 μ thick; epicutis well developed, consisting of thin filamentous hyphae occasionally with an upturned terminal cell, slightly gelatinized; hypodermium denser than the flesh beneath and more deeply colored; hyphae of the context of the pileus short and voluminous, cell walls c. 0.7 μ or less thick, deep ocher brown from incrusting membrane-pigment; clamp connections present.

Chemical characters: guaiac solution, bluing on white portions of context.

Gregarious to cesptitose, rarely solitary on soil or on sugar cane mulch, mostly in shaded places or on rich earth which has recently been moved or altered, fruiting in summer, during the rainy season. Southern United States (Alabama) and Mexico (Oaxaca).

Material studied: U.S.A.: Ala., Montgomery, TYPE (NY). Mexico: Oaxaca, Huautla de Jiménez, *R. Heim* (as *P. caerulescens* var. *mazatecorum* Heim), (NY); *Singer M 1513* (MICH).

Illustrations: V. P. & R. G. Wasson, Mushrooms Russia and History **2**: *pl. 40, fig. 3* (poor); *Life*, May 13, 1957, p. [107], *fig. at upper right*.

Heim first described this fungus as a new species and then, after receiving a letter from Smith suggesting that the species was the same as *P. caerulescens Murr.*, he apparently changed his mind and referred to it as *P. caerulescens* var. *mazatecorum* but gave no immediate critical account of how var. *mazatecorum* was actually different from the type variety. There may be a difference in the taste since that was indicated as mild in the type collection, but until the recent interest in hallucinogenic fungi this species remained known almost entirely from the type collection made by R. P. Burke of Montgomery, Alabama, who wrote "no characteristic taste." It is possible that Burke did not regard a slight astringent taste as distinctive, or that in merely tasting the raw specimens he did not chew the material long enough to bring out the true flavor.

The character of the veil's being more developed in var. *mazatecorum* than in var. *caerulescens*, as Heim emphasized in his Latin description, is dubious because from the description of Burke's collection it is likely that his notes referred to mature specimens and the fact that no veil is mentioned cannot be regarded as conclusive. Hence, there seems to be no way to prove these points except by continued collecting and observing, both in the southern United States and Mexico, to determine eventually the range of variability.

14. PSILOCYBE AGGERICOLA Singer & Smith, Mycologia **50**: 142. 1958. (FIGS. 32–33.)

Pileus 20–40 mm broad when young, campanulate, then conic campanulate or convex, disc at first umbonate, and with a slight umbilicus in the umbo, later with a pronounced central papilla, margin incurved at first but soon straight, strongly hygrophanous and translucent-striate over outer half when moist, estriate when faded, glabrous and naked, except rarely with vestiges of the veil along the margin, colors light olive brown or brown with a darker disc (*oak, Sudan br.* young, disc sometimes *burnt umber,* becoming *khaki* to *Isabella color,* with a *tortoise* colored disc) fading to a dull deep yellow tone (*9 J 6*) when young, to pale chamois (*11 F 4*) when old, tending to blacken when drying.

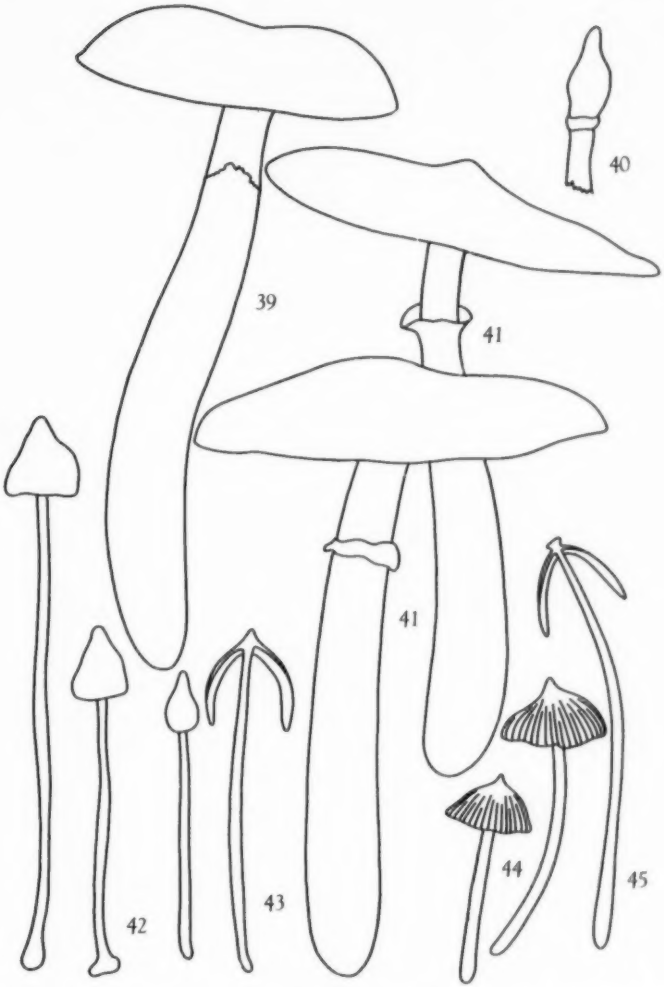
Lamellae narrowly and rather deeply sinuate to adnexed, close or subclose, moderately broad or rather broad and broadest towards the stipe, dingy (olive) brown (*bamboo* to *stag*), trama staining blue where exposed, edges white and entire.

Stipe 25–80 × 6–13 mm, later 2.5–6 mm, tapering upward or finally nearly equal, light ochraceous (*Leghorn*) above, later becoming somewhat *burnt umber,* dingy ocher (*maple*) downward and finally coffee-with-milk color (*Mosul*) in lower half, turning blackish in drying, with a sordid cream to pallid floccose-fibrillose covering which is very conspicuous in young material though fugacious in the upper half (persistent in the lower half) of adult stipes, bluing where injured or on handling, the base white mycelioid; veil forming a fugacious, very narrow annular belt at apex but annulus disappearing at maturity.

Context rather firm at first, more fragile in age, not tough in stipe, light ochraceous (*Leghorn*) becoming coffee-with-milk color (*Mosul*), and turning blue (*Quaker blue, Arctic,* finally reaching *Rigi blue* in dried condition) when either pileus or stipe is bruised; odor none.

Spore deposit deep purple fuscous.

Spores 6.2–8 × 4–5.2 × 3.6–4.5 μ, usually 6.7–7.3 × 4–4.5 × 3.7–4.2 μ, somewhat but little compressed or almost terete (usually 0.3–0.4 μ broader in face than in side view), slightly inequilateral in side view, elliptic-ovate to rarely rhombic in face view, with a broad germ pore, dingy yellow brown in KOH, smooth; basidia (12.5–)14.5–20.5× 4.2–5.5(–7)μ, 4-spored to rarely 2-spored, hyaline or nearly so, clavate to broadest below the apex, basidioles vesiculose-clavate; pleurocystidia 20–32 × 6–9 μ, originating in the subhymenium, contents homogeneous (not protoplasmatic), with a thin colorless resinous incrustation which renders them opaque, varying from clavate to fusoid or ventricose-ampullaceous or constricted in the middle, often with lateral outgrowths or apical nose-like appendages but these lacking in some preparations; cheilocystidia 20–25(–29) × (3.5–)5–5.5(–8.2)μ, usually somewhat ventricose below, upper portion lanceolate narrowed in one or two stages to an acute apex, entirely hyaline and transparent, thin-walled, non-



FIGS. 39–45. 39: *P. candidipes*. 40–41: *P. cubensis*. 42: *P. pelliculosa*. 43: *P. mexicana*. 44–45: *P. yungensis* (44 = var. *acutopapillata*, 45 = var. *yungensis*).

incrusted, causing the gill edge to be heteromorphous; subhymenium when revived in NH_4OH often strongly green from a membrane-pigment, later honey yellow, consisting of a thin layer or irregularly arranged hyphal cells of various shapes; gill trama consisting of elongated subparallel hyphae of variable width and having walls 0.5–0.7 μ thick, the mediostratum not sharply differentiated from the hymenopodium and lateral stratum; epicutis of pileus a thin and not sharply differentiated layer of hyaline hyphae, the hyphae not much gelatinized, when revived in NH_4OH, freshly dried material appearing greenish but later losing all color; hypodermium composed of elements which show very variable shape but not isodiameteric, brownish melleous as revived but hyphal walls not incrusted; clamp connections present.

Chemical characters: formalin on the flesh immediately brownish, not bluing; $FeSO_4$ on flesh, causing a bluish gray ring to appear around a brown spot.

Singly or in small cespitose groups of two or three on rich soil along dammed-up earth of the road, outside the forest in subtropical vegetation, fruiting in spring. Argentina, prov. Tucumán, road to Tafí dell Valle near Monumento al Indio, 900–1000 m altitude, *R. Singer T 760*, 11–13–1949 (MICH).

The opaque pleurocystidia distinguish this species from all similar ones.

15. PSILOCYBE CANDIDIPES Singer & Smith, Mycologia **50**: 141. 1958. (FIGS. 14, 17, 20, 39.)

Pileus 50–55 mm broad, convex with shallowly depressed disc, always obtuse at first, smooth and glabrous, slightly viscid, when moist translucent-striate over the marginal third, sordid buff to dull buff, hygrophanous, fading from the disc outward, pale buff to whitish when faded, readily staining blue when touched.

Lamellae pale avellaneous to avellaneous-gray, sinuate-adnate, rather broad, fairly close to subdistant.

Stipe about 100 mm long, 7–12 mm thick, hollow, nearly equal, readily staining blue, strongly scabrous-strigose near base, and this coating ascending up to mid-portion, increasingly white floccose upward to the annular zone left by the broken veil; veil white, soft, annular, remnants fugacious, but floccons below annular zone rather persistent, readily staining blue where injured.

Context whitish to dingy white, fleshy in pileus, fibrous-hard in the stipe; odor weakly but distinctively farinaceous.

Spores 6.7–7.7 × 3.5–3.8 μ, terete or nearly so, oblong-ellipsoid to ovoid, smooth, wall complex but relatively thin (0.7 μ), both episporium and endosporium differentiated, with a distinct apical germ pore; basidia

4-spored, 13.5–21 × 3.5–6.3 μ (mostly 4–5 μ broad), clavate, not opalescent; pleurocystidia present only as cystidioles, ventricose-submucronate to fusoid-clavate, body of cell often opalescent but neck emerging and non-opalescent, 21–24 × 5–7 μ; cheilocystidia very numerous, lanceolate-fusoid to subulate, hyaline, 18–27 × 3.5–6 μ, upper part narrowed to 1.5 μ or less in diameter, acute to subacute; subhymenium melleous to brown (browner near cap trama), consisting of very small elements often appearing cellular in sections but in reality irregular in shape; gill trama regular, hyaline, in the poorly differentiated mediostratum melleous-hyaline, hyphae not markedly enlarged; epicutis well developed, of only slightly gelatinized narrow (1.3–3.3 μ) hyphae, near surface often giving rise to a cystidioid end-cell which is not gelatinous; velar floccons of stipe everywhere consisting of very irregularly shaped cells of various sizes either inflated or filamentous and strongly interwoven, frequently cystidioid cells arising from the surface hyphae of the velar material, these c. 20 × 5 μ and ampullaceous, apex 2 μ broad; clamp connections present.

Chemical characters: Several chemical substances accelerate and augment the bluing, especially guaiac solution.

On earth, cespitose, among fallen leaves of *Coffea* and *Inga* along irrigation ditches in plantations. Mexico, Oaxaca, Huautla de Jiménez, 1550 m altitude, *R. Singer M 1514*, 7–10–1957, TYPE (MICH).

The small terete spores, strong tendency to turn blue, and copious veil are an interesting set of characters in this genus. The strong development of the veil is a valid additional argument for including the stirps *Cubensis* in this genus. Weight is added to this argument by the fact that in *P. cubensis* the same kind of dermatocystidia are often found on veil and pileus. The two, of course, differ sharply in spore characters.

The young hymenium, typically hymenium just beginning to sporulate, is very interesting in view of the bluing phenomenon. The basidia and basidioles are incrusted with blue granules. The young cystidioles (obviously formed earlier in the development of the hymenium) are not. Does this mean that the early development of these cells did not include the production of the enzyme that causes the formation of the blue pigment? Also, does it prove that those cells which are destined to remain sterile are differentiated physiologically before morphological differences become evident?

16. PSILOCYBE ZAPOTECORUM Heim, Rev. de Mycol. **22**: 77. 1957.

Pileus 60–110 mm broad, campanulate becoming obtusely umbonate to strongly mammillate but always twisted, asymmetric, most variable

in shape, margin at first white punctate with the veil remnants, (soon) glabrous, color varying from ochraceous citrine to purple-brown-black (Klingcksieck et Valette no. 45) with ochraceous-melleous tones, with dark violet stripes and gradually becoming violet black on margin, apparently hygrophanous and dingy melleous when faded.

Lamellae rather close, with sinous edges, adnexed-emarginate, not very broad, violet-purple.

Stipe 100–200 mm long, 10–20 mm broad at base, hollow, very fibrous, hard, elastic, often contorted, outer layer of cortex brownish, ochraceous toward the interior and with a central soft white bluing pith, (surface) fibrillose.

Context at first brown-rufous in cortex of stipe, yellow in central portion, entirely and quickly bluing; odor farinaceous; taste astringent.

Spore deposit brown-purple.

Spores 6–8.8 × 3.5–5 × 3–4 μ (Heim **1957**), rather bright yellow revived in KOH, somewhat compressed, with a broad apical germ pore; cheilocystidia fusoid, with a filiform neck which is covered by a substance stained by dyes (such as "bleu lactique").

On swamp soil, Yaitepec and San Agustin de Loxicha, Oaxaca, Mexico. Used as hallucinogen by the Chatino and Zapotec Indians, known as "mbey san" or "piule de barda" (according to Heim).

Illustration: *Life*, May 13, 1957, p. [107], *fig. at upper left.*

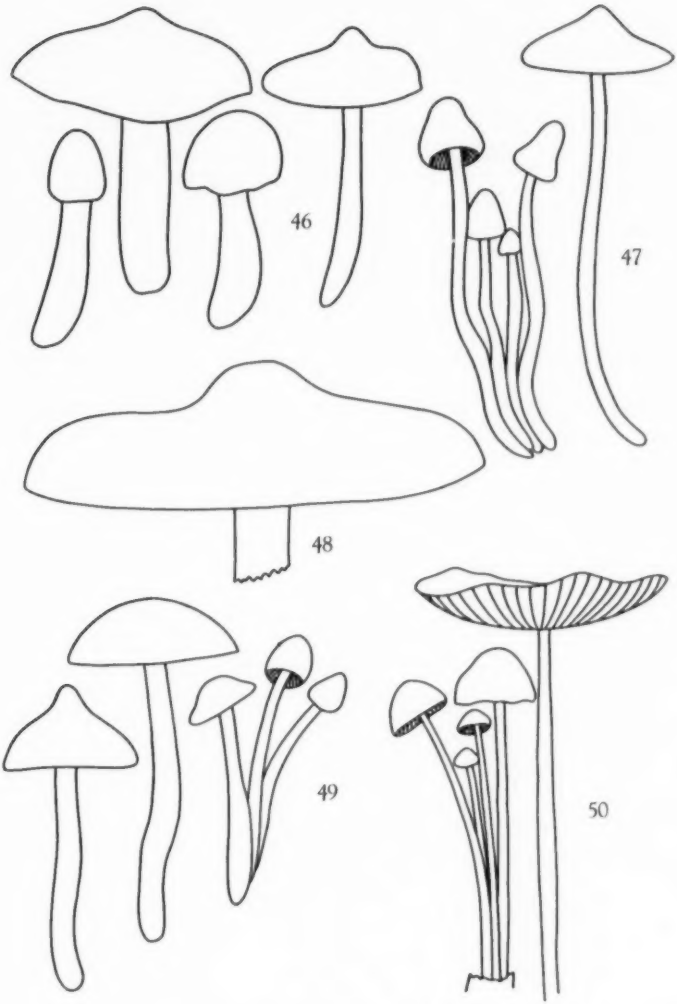
Material studied: None. The above incomplete description is based on fragmentary data and a Latin diagnosis furnished by Heim. Probably there are specimens at Paris.

The habitat is not particularly strange for a *Psilocybe* as far as North American members of the genus are concerned; therefore, it is rather a surprise to find that Heim considered it so. A relatively tough context of the stipe is likewise not unusual in the genus, and it may only be relatively more so in *P. zapotecorum*. Nevertheless, it is possible that this species does not belong with the preceding species. We do not wish to judge its final relationships without having had a chance to study specimens.

STIRPS CAERULIPES

17. PSILOCYBE MULIERCULA Singer & Smith, Mycologia **50**: 142. 1958. (FIGS. 34–35, 49.)

Pileus 20–35 mm broad or more, campanulate then convex, eventually often applanate in a zone between the umbo or papilla and the somewhat decurved marginal area, more or less umbonate, rarely papillate, fulvous brown, hygrophanous, fading out to a pale ocher tone,



FIGS. 46–50. 46 and 48: *P. caerulescens*. 47: *P. caerulipes*. 49: *P. muliercula*. 50: *P. strictipes*.

glabrous, not viscid, marginal area translucent-striate (up to about half way to disc) when moist, slightly sulcate at times, naked.

Lamellae fuscous-sepia, almost narrow, ascendant to subhorizontal, sinuate-adnate, often seceding, with pallid edges.

Stipe (30–)40–100 × 2–7 mm, equal or tapering upwards, becoming hollow, sordid flesh-colored-whitish, becoming concolorous with the pileus especially below, staining blue where touched and blue stains eventually very deeply colored, smooth, more or less glabrous and naked; veil very sparse and all traces of it obliterated in mature specimens.

Context tending to turn blue where injured; odor farinaceous; taste in dried specimens not distinctive.

Spores (6–)7–8(–10) × 4.2–4.8(–5) × 3.9–4.7 μ, either terete or up to 0.3 μ broader in face view than in side view, elliptic to elliptic-ovate in either view, rarely subrhomboid with rounded angles in face view, sometimes ventricose-fusoid (shaped like a bolete spore) in side view, with a distinct apical germ pore, dark yellowish brown in KOH; basidia 16.5–21 × 5–5.5 μ, 4-spored; pleurocystidia none; cheilocystidia 12–23 × 3–5.5 μ, hyaline, subulate to subulate-ampullaceous, apex obtuse and sometimes subcapitate, more often subacute or acute, neck at apex 1.5–2 μ in diameter; subhymenium a thin layer, irregular, of small elements; gill trama regular, walls of hyphae up to 1.5 μ thick (thick-walled for the genus); epicutis a well developed layer of hyaline filamentous hyphae but not strongly gelatinized; hypodermium well colored by membranal pigment often incrusting the walls of the hyphae, the latter arranged into a compact layer or a cutis; hyphae of context and hypodermium with thickened (about 1.5 μ) walls; clamp connections present.

Solitary or in small clusters on earth along ravines of a pine-covered (*Pinus pseudostrobus*) mountain at about 3000 m elevation; fruiting in late August and September, rarely before. Known only from the slopes of Cerro Toluca (Mexico).

Material studied: Mexico, purchased at the market of Tenango del Valle (Toluca Valley), September 30, 1956, *T. Herrera* (MICH, MEX); September 1957, *G. Guzmán* (MICH, MEX); purchased at Piedras Blancas, Cerro Toluca, July 30, 1957, *R. Singer M 1011*, TYPE (MICH).—There must be material of this at Paris since it was sent by T. Herrera to Heim, purchased at the same place and apparently identical with material earlier purchased in Tenango by the Wasson group and determined as *P. mexicana* var. *brevispora*.

This species is quite different from all other known species, particularly from *P. mexicana* which has larger spores and a more typically *P. semilanceata*-like habit.

18. PSILOCYBE CAERULIPES (Peck) Sacc., Syll. Fung. **5**: 1051. 1887. (FIGS. 36–38, 47.)

Agaricus caerulipes Peck, Ann. Rep. N. Y. State Mus. **38**: 89. 1885.

Pileus 10–35 mm broad, when young obtusely conic to convex and with an incurved margin, becoming broadly convex to plane or retaining a slight umbo, at times quite irregular, surface glabrous, viscid, soon dry and shining, closely translucent-striatulate and watery cinnamon brown to dingy "Sayal brown" fresh, hygrophanous and soon fading to dingy ochraceous buff or cinnamon buff, sordid alutaceous in age and often with greenish stains along the margin or with a greenish tinge overall.

Lamellae sordid brown when young, becoming rusty cinnamon, close or crowded, narrow, adnate or arcuate-adnate or with a decurrent tooth, edges whitish and slightly fimbriate.

Stipe 30–60 mm long, 2–3 mm thick at apex, equal or slightly enlarged downwards, stuffed with a pith but becoming tubular or hollow, the pith fairly persistent, surface pruinose at or near the apex, downward appressedly white to grayish fibrillose, usually staining greenish blue where handled, whitish to buff at first, especially above, pallid to bluish when dried, lower part often dingy brown in age; veil whitish, thin, forming an evanescent superior fibrillose zone; basal mycelium white.

Context in pileus thin and pliant, in stipe tough, in both becoming bluish when injured; odor none; taste farinaceous.

Spore deposit very dark purple brown.

Spores 7–9.8 × 4–5.3(–5.7) × 4–5.1 μ, usually 8–8.5 × 4.4–5 μ, but those from 2-spored basidia 10–11.2(–12) × 5.7 μ, generally terete, only a small minority very slightly broader in face than in side view, ellipsoid, or elliptic in face view and inequilateral in side view, pale tawny to olive fuscous in KOH, truncate with an apical pore, smooth; basidia 15–28 × 5.2–7.5 μ, either all 4-spored, or some 2-spored, often constricted in mid-portion, hyaline in KOH; pleurocystidia none, or present only near gill edge, and then similar to cheilocystidia; cheilocystidia forming a broad sterile band at gill edge (which is heteromorphous), 18–35 × 4.2–6.7 μ, hyaline, with homogeneous contents, narrowly fusoid-ventricose, subulate, or ampullaceous, neck 1–2.2 μ broad and, if ampullaceous, 7–20 μ long, the tip sometimes slightly thickened to almost subcapitate (1.7–2.2 μ diameter), otherwise acute to obtuse, sometimes bifurcate; subhymenium seemingly cellular, but consisting of very irregularly shaped generally rather short very small elements, stramineous-melleous; hymenopodium of axial filamentous light stramineous-melleous hyphae 2–6.5 μ in diameter; gill trama not clearly differentiated in mediostratum and lateral stratum, regular, consisting of elongated hyphae 6–24 μ thick with 0.7–1.5 μ thick walls, melleous hyaline varying

to pale brownish (in KOH); epicutis a gelatinous pellicle, not very broad, consisting of 2–4.5 μ thick hyaline (rare individual hyphae sometimes stramineous) filamentous hyphae which are loosely arranged; dermatocystidia none; hypodermium more irregular than epicutis, forming a cutis of compactly arranged short hyphal cells with brownish walls, but without any conspicuous incrusting pigment, hyphae 6–12 μ in diameter; this layer gradually merging below into the paler interwoven floccose trama of the pileus; clamp connections present.

Solitary or cespitose on debris of hardwood trees, especially *Betula* and *Acer* but also on their logs rotting on the ground. It fruits during the summer, more rarely in fall in the eastern and mid-western states of the U.S.A. and in Canada (Ontario), south to North Carolina.

Material studied: Canada, Ontario: Petawawa Exp. Forest, *Smith 26312* (MICH). U.S.A., Maine: near Guerette, *Bigelow 3531* (MICH). New York: Catlin Lake, Adirondack Mts., *Smith 219* (MICH); *C. H. Peck*, TYPE (NYS, NY). North Carolina: Indian Creek, Great Smoky Mts., *Hesler 10166* (MICH); *Smith & Hesler 17415* (MICH). Flat Creek, *Smith 10586* (MICH). Ohio: Cleveland, *Walters 186* (MICH). Tennessee: Grassy Patch, Great Smoky Mts. Nat. Park, *Smith 10545* (MICH). Michigan: Pontiac, *Smith 7268* (MICH); common around Pellston, Mackinaw City, *Smith 22186, 23459, 23460, 32893, 33648, 33824, 33825, 33933, 35872, 42103, 43053* (all MICH); *Thiers 3523* (MICH); Taquamenon Falls State Park, *Smith 36916, 37181, 37428, 39442, 41656, 41721, 41722, 41985, 41988, 42235, 49910, 49934, 49935, 49936, 49948, 49952, 49967, 50312; Thiers 3214* (all MICH).

The blue to greenish stains may be slow in developing but they usually show in a few hours.

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NOTES AND BRIEF ARTICLES

Two Unrecognized Species of Cytidia

In a recent treatment of the genus by Cooke (Mycologia **43**: 196–210. 1951), *Cytidia* and its kindred genus *Aleurodiscus* are characterized by their very large basidia and basidiospores, and by the distinctive, sterile, dendrophysoid structures present in the hymenium. *Cytidia* is further distinguished by its strongly gelatinized hyphae forming the cup-shaped basidiocarps. *Stereum*, as typified by *S. hirsutum* (Willd. ex Fr.) S. F. Gray and its relatives, possesses none of these features. Two species of *Stereum* described by Burt (Ann. Mo. Bot. Gard. **7**: 81–238. 1920) have all of the characters essential for *Cytidia*. Obviously, these species cannot be retained within *Stereum* but must be transferred to *Cytidia*.

Cytidia patelliformis (Burt) comb. nov. Fig. 1.

Stereum patelliforme Burt, Ann. Mo. Bot. Gard. **7**: 182. 1920.

Basidiocarps lignicolous, hard-brittle when dry, rapidly absorbing water when soaked, resupinate to open cup-shaped, 5–20 mm long, 3–9 mm wide, some fructifications with confluent margins, superior surface from yellow-buff to dark reddish-brown, strigose with matted white hairs in well-developed receptacles, hymenial surface pink to dark reddish-brown, pulverulent to setulose under the lens.

Receptacle 525–700 μ thick in free-hand section; cuticle absent to poorly developed; context and hymenium forming the only two zones generally present; context interwoven with the hyphae turning outward to form the superior surface of the receptacle and the hymenium, in resupinate forms only the hyphae next to the substrate densely interwoven, then radiating outward forming the hymenium at their tips; hyphal walls somewhat thickened and strongly gelatinized, bearing numerous and prominent clamp-connections, branching, 4–6 μ diam.; subhymenial hyphae similar but with thinner walls, 3–4 μ diam.; cystidia projecting up to 60 μ above the hymenial surface, cylindrical or tapering slightly, a few with swollen apices, non-septate, unincrusted, thin-walled, 7–8 μ diam.; basidia 56–80(–108) × 6–8 μ, often projecting 10–11 μ above the hymenial surface, with four fleshy, arcuate sterigmata, each 6–8 μ long; sterile dendrophysoid structures intermingled among the basidia, 2–3 μ diam.; crystalline material present in context and hymenium; spores hyaline, even, slightly curved, apiculate, 10–15 × 4–5 μ.

SPECIMENS EXAMINED: Washington: *W. N. Suksdorf 713*, TYPE of *S. patelliforme, 884, 917; W. B. & V. G. Cooke 18853, 22593, 22706, 26212* (all WSP); New Mexico: *Paul C. Standley*, Mo. Bot. Gard. Herb. 44951 (BPI). A note on the New Mexico packet, presumedly by Burt, comments on its similarity to *Corticium salicinum* (*Cytidia salicina*). Burt also lists *Suksdorf 752* from Washington (WSP) but since only a very small amount of this material was present, no microscopic examination was made. Macroscopically it agrees well with the other specimens of *S. patelliforme*. *Suksdorf 753* (also listed by Burt)

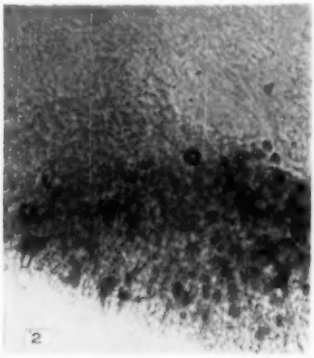

FIG. 1. *Cytidia patelliformis.* Microphotograph of a free-hand section through the basidiocarp. Note the protruding unincrusted cystidia and the interwoven, gelatinously modified hyphae. Approx. × 135.

FIG. 2. *Cytidia magnispora.* Microphotograph of a free-hand section through the basidiocarp. Note the embedded and protruding, incrusted cystidia and the interwoven, gelatinously modified hyphae. Approx. × 135.

is not *S. patelliforme*. It appears to be immature, but the hyphae with their ampulliform swellings are characteristic of neither *Stereum* nor *Cytidia*.

Cytidia magnispora (Burt) comb. nov. FIG. 2.

Stereum magnisporum Burt, Ann. Mo. Bot. Gard. **7**: 207. 1920.

Basidiocarp hard-brittle, probably somewhat waxy when fresh, attached broadly to the substrate and with upturned, free margins which give a cup-like appearance to the fructifications, up to 5 mm wide and 17 mm long, margins frequently coalescing, upper surface light buff to white, minutely tomentose, hymenial surface dark buff with pink tinges, setulose, occasionally folded or veined.

Receptacle 750–900 μ thick in free-hand sections; cuticle absent or poorly developed; context and hymenium forming the only two zones generally present, although the superior surface may show a layer of thicker walled, more densely entangled hyphae; contextual hyphae hyaline, branching, with clamp-connections which are often difficult to distinguish because of the thick, gelatinous matrix in which the hyphae are embedded, interwoven, 2–3 μ diam.; subhymenial hyphae similar; cystidia projecting up to 40 μ above the hymenial surface, or embedded, heavily incrusted with hyaline granules for three-fourths of their length, thick-walled, with pointed or tapering tips, 48–91 × 16–21 μ; basidia 57–72 × 16–19 μ, with four fleshy, arcuate sterigmata, each 8 μ long; hyaline, dendrophysoid structures prominent in the hymenium, often associated with granular matter; spores hyaline, smooth 17–21 × 14–17 μ.

SPECIMENS EXAMINED: Jamaica: *W. A. & E. L. Murrill 328,* TYPE of *S. magnisporum, 522* (both FH-C).

While *C. patelliformis* and *C. magnispora* both possess cystidia, they do not seem to be closely related. The receptacular hairs and spore size of *C. patelliformis* place it close to *C. salicina* and *C. sarcodes.* The lack of such hairs in *C. magnispora* closely associates this species with *C. pezizoides* and *C. simulans,* but it is distinct from them because of the presence of cystidia and the larger spores. The two species discussed here fall into the section *Lomatina* (Karst.) W. B. Cooke.

I wish to express my appreciation to Dr. I. MacKenzie Lamb, Director, FH-C, Dr. Charles Garner Shaw, Curator, WSP, and Mr. John A. Stevenson, Principal Mycologist, BPI, for their generous loan of specimens.—ARTHUR L. WELDEN, Tulane University, New Orleans 18, Louisiana.

ON HYDNUM CHRYSORHIZUM TORREY

Eaton, in the first edition of his Manual of Botany for the Northern States, 1817, p. 140, published the name *Hydnum chrysorhizum* Torrey. In the third edition, 1822, p. 309, this was again published, with the following description: "yellow, membranaceous, stemless, spread; root golden-yellow, filiform, with intersecting branches; extending far along the grains of decaying wood. The root of this fungus has often been noticed several yards in length; but Dr. J. Torrey, of New York, was the first, I believe, who traced it to the pileus, and proved it a *hydnum.*"

This name seems to have been completely overlooked by later students of the group. The type of Torrey's species is in the Torrey Herbarium, now preserved in the New York Botanical Garden. It consists

of several portions of the hymenium with the separable context, 40–50 sq cm in area, glued to the sheet above, and below a generous example of the rhizomorphs. The hymenial surface is now brownish and the rhizomorphs are pallid, but there can be no doubt that this is the same as *Hydnum fragilissimum* Berk. & Curt. 1873, later called *Oxydontia fragilissima* (Berk. & Curt.) Miller, and *Mycoacia fragilissima* (Berk. & Curt.) Miller & Boyle. Except for the color, which fades quickly in this species, it agrees in all particulars. The teeth are the same, there is an abundance of spores of correct size, and the thick, encrusted hyphae in the rhizomorphs are precisely the same as those found in more recent collections. In all mounts there are bacteria and mold spores

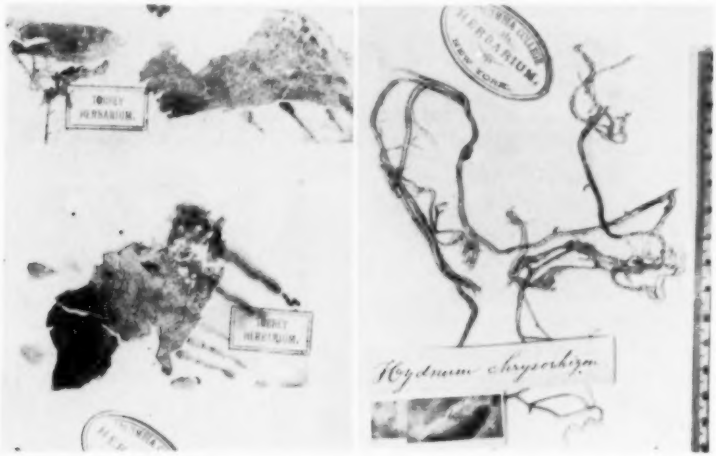

FIG. 1. Herbarium sheet, from Torrey Collection, New York Botanical Garden, bearing type specimen of *Hydnum chrysorhizum*.

present, particularly truncate, subglobose, echinulate spores of what is probably an *Aspergillus*. The original description gives the color as yellow, the rhizomorphs golden yellow. All specimens seen when fresh have been orange to orange-red. Despite this statement, the evidence of the specimen in the New York Botanical Garden (FIG. 1), here designated as the lectotype, is entirely convincing.

Lloyd (Myc. Writ. **4**, Letter 53: 11. 1914) called this species *Odontia crocea*, based on *Sistotrema croceum* Schw. (Schr. Nat. Ges. Leipzig **1**: 102. 1822). This may have been applied to the present species, as may have the following species on the same page, *S. cinnabarinum*

Schw. Lloyd states that he found no specimen of *croceum* in the Schweinitz herbarium. His only reference to *cinnabarinum* (Myc. Writ. **3**, Letter 35: 3. 1911) comments on a South African collection with small globose spores.

The genus *Mycocia* cannot be used in the sense of Miller and Boyle; the earlier proposal by Miller (Mycologia **25**: 294. 1933) to group the *Odontia*-like species lacking cystidia in *Oxydontia* has much merit.

We therefore propose the following new combination and list the synonymy.

Oxydontia chrysorhiza (Torrey) comb. nov.

Hydnum chrysorhizum Torrey, in Eaton, Manual, ed. 3, 309. 1822; *Hydnum fragilissimum* Berk. & Curt. Grevillea **1**: 100. 1873; *Hydnum ischnodes* Berk. Grevillea **1**: 101. 1873; *Hydnum chrysocomum* Underw. Bull. Torrey Club **24**: 82. 1897; *Acia chrysocoma* (Underw.) Pat. Essai Tax. Hymen. 69. 1900; *Odontia crocea* sensu Lloyd. Myc. Writ. **4**, Letter 53: 11. 1914; *Oxydontia fragilissima* (Berk. & Curt.) Miller, Mycologia **25**: 364. 1933; *Mycoacia fragilissima* (Berk & Curt.) Miller & Boyle, Univ. Iowa Stud. Nat. Hist. **18**(2): 42. 1943.—DONALD P. ROGERS, University of Illinois, and G. W. MARTIN, State University of Iowa.

REVIEWS

MONOGRAFIA UREDINALELOR DIN REPUBLICA POPULARĂ ROMÂNĂ, by Traian Săvulescu. Vol. I and II. 1166 pp., 53 pl., 948 text figs. Acad. Repub. Pop. Române, Bucuresti, 1953.

These volumes are in the Rumanian language. The first six chapters of Vol. I are devoted to such general topics as morphology, life cycles, specialization, effect of the parasite on its host plant, hyperparasites of the rust fungi, distribution of the rust fungi in Rumania, and a brief review of some generic classifications, including Dietel's (1928) system, which is followed in Vol. II. Chapter seven, comprising pp. 141–280, 52 plates and a 49 page bibliography, is devoted to the rust diseases of economically important plants. There are 84 pages devoted to cereal rusts. There is an "Anexă" consisting of pp. I–XXIV and 22 fold-out tables in which is tabulated for 360 varieties of wheat the percentage of rust (leaf or brown rust, stripe rust, and stem rust) for each of 10 years in the period 1936–1949. It is doubtful if the data presented are particularly significant and, on the whole, the "Anexă" is not a valuable addition.

The second volume is devoted to a systematic presentation, including synonymy, descriptions, keys and illustrations. The illustrations of species are original line drawings and are excellent. Keys to species are apt to be none too good but Săvulescu's are particularly inadequate where the need is greatest, e.g. the species of *Puccinia* on grasses and composites. In the grass rusts, for example, he separates the species which have covered telia from those with exposed telia, then the coronate species from the non-coronate, but from there one must know not only the telial host but also the aecial. Similarly, under the Compositae there is one group of 27 species where the only "character" employed is the name of the host plant.

Prof. Săvulescu's treatment of certain species is quite unlike that of Arthur's "Manual." He recognizes *Puccinia phlei-pratensis* Eriks. & Henn. and *P. anthoxanthi* Fckl. as distinct from *P. graminis* Pers. and in the leaf rust (brown rust) complex he segregates 13 species from what Arthur treated as *P. rubigo-vera* (DC.) Wint. (= *P. recondita* Rob. ex Desm.) but he is generally following European custom in this.

This treatise undoubtedly meets not only a local but a regional need. It is the first descriptive manual to be published in Europe in many

years and therein lies its principal interest and use to extra-European mycologists and pathologists.—GEORGE B. CUMMINS.

USTILAGINALELE DIN REPUBLICA POPULARĂ ROMÎNĂ, by Traian Săvulescu. 2 vols., 1168 pp., 21 pl. (color), 594 text figs. Acad. Repub. Pop. Romîne, Bucuresti, 1957.

Volume I of Săvulescu's Ustilaginales of Roumania deals with the general biology of the smuts and is organized into 14 chapters. Chapters I–IX are devoted to the basic aspects of the smut fungi, while Chapters X–XIV present comprehensive treatments of specific smut diseases, as regards their causal agents, symptoms, and control. Each type of smut is illustrated in color, both as to symptoms and spore germination. The color plates are reproductions of drawings, expertly and artistically done, to depict disease symptoms and spore characteristics, including the germination process. The text figures include drawings, photographs, graphs, and charts. About half of these are photographs and the other half are drawings.

In Chapter I the author treats the "Morphology of the Ustilaginales" under four main sections, covering 63 pages. The first of these sections deals with the mycelium, giving full consideration to the nuclear aspects in the diploid and haploid stages. The second section is on fruiting structures, the author describing briefly the different types of sori while discussing at length the chlamydospores (teliospores), including their formation, shape, size, and other characteristics. At this point also the author considers factors affecting spore germination and the growing of smut fungi in culture. Further in the second main section of Chapter I the author also treats the morphological and cytological changes that occur during spore germination and gives special consideration to the varied terminology applied by different authorities to the end products of spore germination. The remainder of this section is devoted to the different types of promycelia (*Ustilaginaceae* and *Tilletiaceae*) and to sexuality (homothallism and heterothallism). In the third main section of Chapter I, the author describes and illustrates with charts the different types of life cycles in the smuts, while the fourth and last section deals with hybridization.

Physiologic specialization is covered in three pages (Chapter II), and 9 pages (Chapter III) are used to treat modes of infection in both natural and artificial inoculation. Smut resistance in host varieties is discussed in Chapter IV, which occupies 9 pages. A bibliography of 993 titles pertinent to the first four chapters is a part of Chapter IV.

In Chapter V (15 pages) the author discusses the effects of smuts on their host plants from the aspects of morphology, cell structure, histology, physiology, and biochemistry. Under physiology and biochemistry he includes respiration, assimilation, transpiration, and chemical constituents. There is a bibliography of 91 titles. Chapter VI (6 pages, including a bibliography of 58 titles) is devoted to the problem of toxicity of the *Ustilaginales* to animal life.

The ecology and geographic distribution of the *Ustilaginales* is treated in Chapter VII. This is primarily a classified grouping of Roumanian species on the basis of host type and habitat. There are 9 categories, including (1) those that occur on cultivated plants; (2) those that occur on weedy plants; (3) those that occur on plants growing in marshy areas; (4) those that occur on aquatic plants; (5) those that occur on plants growing in coastal areas; (6) those that occur on pasture plants; (7) one species that occurs on *Juniperus nana;* (8) those that occur on woodland plants; and (9) those that occur on plants growing in alpine and sub-alpine areas. Additional features of Chapter VII are (1) a distribution tabulation of the smut genera in 10 different countries of the world; (2) a distribution chart of host families for the smut genera occurring in Roumania; and (3) a species listing by seven continental areas, with their respective percentages of the total smut species population of Roumania. A bibliography of 64 titles concludes this Chapter of 16 pages.

Chapter VIII (13 pages and 54 bibliography titles) is on the classification of the *Ustilaginales* and contains a key to the families and genera. This chapter also deals with phylogeny. Chapter IX, one-half page long, is on the fungus parasites of the *Ustilaginales.*

Chapter X, the longest of the volume (307 pages), is devoted to the smuts of cereal crops. These are treated in host groupings, with a bibliography at the end of each section on a specific smut. With a few exceptions each smut is discussed under the general organizational pattern of common name, symptoms, economic importance, etiology, mode of infection, specialization, varietal resistance, and control. In the case of bunt or stinking smut of wheat, the organization deviates from the basic pattern to treat the different species from several additional aspects, including cytology, genetics, factors affecting spore germination in the laboratory, and spore formation in culture. Perhaps this lengthy treatment of wheat bunt (141 pages and a bibliography of 588 titles) is indicative of its relative economic importance in Roumania. The entire chapter has a total of 1401 bibliography titles.

Chapter XI, in 13 pages, deals with the smuts of certain feed crops,

especially millet and tall oatgrass. This chapter also carries a list of grass hosts for species of *Ustilago, Sphacelotheca, Urocystis,* and *Tilletia.* A similar treatment is given to the smuts of industrial, medicinal, and garden plants in Chapter XII (11 pages and 41 bibliography titles). All of Chapter XIII (5 pages, with 40 bibliography titles) is devoted to onion smut. In Chapter XIV, just four sentences long, the author takes cognizance of a smut on *Juniperus nana* Willd.

It would seem that Volume I is somewhat "cluttered" with tables, some of which are so long as to be unwieldy. There are 88 tables ranging in length from less than half a page to as many as six pages. Some of the longer tables require over-size pages, which must be folded to keep them within the over-all dimensions of the volume. As a convenience to the reader, these might well have been avoided.

The entire bibliography of Volume I lists 2761 titles.

Volume II is a mycological treatment of the *Ustilaginales,* including the families, genera, species, varieties, and forms and their synonyms. The basic organization includes descriptions, geographic distribution in Roumania and throughout the world, critical observations, and illustrations. For illustrations the author uses photographs of the diseased host and drawings of the smut spores.

The volume begins with a brief description of the *Ustilaginales* and a key to the three families the author recognizes. This is followed in turn by brief descriptions and keys to the various families, genera, and species. There is a bibliography at the beginning of the treatment of each taxonomic unit.

Volume II, being strictly a mycological treatise, should find considerable utility among American workers, despite the language barrier. The short, simple phrases used in taxonomic keys and descriptions are translatable to a usable extent, with the aid of a Roumanian-English dictionary. Furthermore, the extensive bibliography accompanying each taxonomic unit will be most helpful to the mycologist, as will also the tabular data on size of spores and other structures, such as sori. Likewise the illustrations can be put to good use in mycological studies.

The number of species treated is considerably augmented by the author's liberal species concept. Physiological, or host, definition of species certainly runs rampant in this work. A good example of this is found in the common anther smut, usually called *Ustilago violacea* (Pers.) Roussel. This smut is treated under nine binomials: *U. violacea,* on *Saponaria officinalis; U. lychnis-dioicae* (DC.) Liro, on *Melandrium* spp.; *U. dianthorum* Liro, on *Dianthus deltoides; U. antherarum* Fries, on one species each of *Dianthus, Silene, Arenaria* and

Minuartia; U. superba Liro, on *Dianthus superbus; U. coronariae* Liro, on *Lychnis floscuculi; U. silenes-nutantis* (DC.) Liro, on *Silene nutans; U. silenes-inflatae* (DC.) Liro, on *Silene inflata* and *Viscaria vulgaris;* and *U. stellariae* (Sow.) Liro, on *Stellaria holostea* and *S. graminea.* The mean spore dimensions of all of these range roughly from $6 \times 7\ \mu$ to $7 \times 9\ \mu$, and the exospore markings are the same in all (*i.e.*, reticulate). Each of the nine species is illustrated by beautiful drawings of 60–80 teliospores each and (with the possible exceptions of *U. silenes-inflatae*) each could substitute for any one of the other eight. Likewise the common flag smut of wheat and grasses is treated under seven binomials. The morphological analyses of each of these emphasize their very close morphological similarity. This reliance on the host for identity of the smut is reflected in the keys. Thus, in the key to the 34 species of *Entyloma* in Roumania, 11 of the binomials under the genus, all on hosts of the Compositae, are keyed out on the basis of 11 different host genera in the same family. However, Dr. Săvulescu is perfectly entitled to employ a host delimitation of species if he wishes, even if many of his colleagues feel that such a concept is taxonomically infeasible.

Disregard for certain rules in the International Code of Botanical Nomenclature is evident. For example, Săvulescu uses the binomial *Tilletia tritici* (Bjerk.) Wint. for the common wheat bunt. The specific epithet is derived from Bjerkander's pre-Persoonian *Lycoperdon tritici* (1795). The binomial applied to one of the segregates of dwarf bunt of wheat recognized by Săvulescu is *Tilletia nanifica* (Wagner) Savul. Here, the specific epithet is taken from Wagner's trinomial, *Tilletia tritici nanifica* (not *tritici-nanifica* as Săvulescu gives it), which Wagner suggested (without formal description, Latin diagnosis or designation of a type) for what he believed to be merely a form of *T. tritici.* Again, the binomial applied to common corn smut is *Ustilago zeae* (Beckm.) Unger, deriving the specific epithet from the pre-Persoonian *Lycoperdon zeae* Beckman (1768).

In view of the prodigious effort involved in its producton, and in the face of the language barrier, it would be imprudent to register more than token criticism of this work. There is no question of its value but its usability could have been enhanced by better organization, especially in Volume I. The 14 chapters in this volume range in length from four lines (!) to 307 pages. The need for several chapter categories of five pages or less is questionable, as these might well have been included in a single miscellaneous category, with appropriate sub-headings. On the other hand, Chapter X is unduly long, covering more than half

of the volume. This tends to reduce materially the ready accessibility of the information, which might better have been organized into several chapter categories.

Although one of the commendable features of these volumes is the generous allotment of space to illustrations, much of this space is wasted on poor quality or unnecessary pictures. Many of the photographs, especially those in Volume II, lack contrast and fail to depict detailed characteristics of the smut disease in question, which was the purpose of their inclusion in the first place. In some cases (wheat bunt, for example) the same smut (species) was illustrated twice (and with the same photograph), seemingly without reason. Along this same line the author was overly generous in illustrating the spore characteristics of the different species with drawings of as many as 100 spores each, when a much smaller number would have served the purpose just as well. Reduced tones would have enhanced the color plates in Volume I.

This two-volume contribution stands as a monument to the productivity of the author, whose diligent and painstaking attention to detail is self-evident in the extensive coverage of the subject matter. However, because of the language barrier, its content in detail will unfortunately remain obscure to the great majority of English-speaking plant pathologists and mycologists. For these workers it will serve mainly as a reference work, primarily to literature on the smuts and, to a lesser extent, also on such general categories as symptom expressions, spore characteristics, host range, nuclear phenomena, and such other phases as it may be possible to interpret from tabulations, illustrations, and chapter sub-headings. This is especially true of Volume I. Volume II is more immediately useful to the taxonomist.

On the whole this work, "The Ustilaginales of Roumania," is an important contribution worthy of a place in all botanical libraries, especially those where teaching is done.—C. S. HOLTON AND GEORGE W. FISCHER.

MANUSCRIPT

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